Context-dependency and complexity of plant-herbivore interactions in fragmented forests

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Preface

For centuries, humans extensively used and profoundly altered ecosystems at a global scale (Chapin *et al.* 2000, Sala *et al.* 2000). As a result, today's world experiences an ongoing *Global change* including habitat destruction, climate change, exploitation of resources and environmental pollution (Chapin *et al.* 2000, Sala *et al.* 2000, MEA 2005). Recently, the United Nations General Assembly designated the year 2011 as *The International Year of Forests*. This initiative reflects the awareness of scientists and policy makers regarding the pervasive human impact on forest ecosystems and the intention to draw public attention to this issue of global concern. The major threat to forest ecosystems is deforestation that proceeds at an alarming rate of 13 million hectares per year (FAO 2010, Ciccarese *et al.* 2012). The main reasons for the deforestation are worldwide population growth as well as economic and industrial development, which demand the conversion of forests into agriculturally used land and the expansion of urban areas (Sala *et al.* 2000, MEA 2005, Jha & Bawa 2006).

Deforestation predominantly drives the fragmentation of forests, which in turn, is expected to entail multifaceted and severe consequences for forest ecosystems and human well-being, *i.e.* with respect to overall biodiversity, trophic interactions, key ecological functions of species and ultimately, ecosystem services of forests (Chapin *et al.* 2000, Sala *et al.* 2000, Tscharntke *et al.* 2012). Amongst others, herbivorous insects are assumed to directly respond to forest fragmentation, which may have serious implications for insect herbivory and thus, plant performance in forest ecosystems (*e.g.* Rao *et al.* 2001). However, current uncertainty regarding the impact of forest fragmentation illustrates the need to further unravel potential shifts in plant-herbivore interactions and the associated process of insect herbivory in fragmented forests (*see* Magrach *et al.* 2014).

Chapter 1

General introduction

Forest fragmentation drives species loss & impairs ecosystem functioning

Deforestation creates human-modified landscapes that differ in their composition and configuration from unmanaged ecosystems and confronts species with a multitude of changes in their environment (Ewers & Didham 2006, Fischer & Lindenmayer 2007, Tscharntke *et al.* 2012). From a landscape perspective, deforestation predominantly reduces the overall amount of forest cover, amplifies edge effects and causes the breaking apart of continuous forests into small forest remnants, termed forest fragmentation (Fahrig 2003, Ewers & Didham 2006, Tscharntke *et al.* 2012, Ibáñez *et al.* 2014). In turn, forest communities suffer a shortage of the amount and diversity of resources that are specific to forest ecosystems (Fahrig 2003, Ewers & Didham 2006, Ibáñez *et al.* 2014). Moreover, particularly less mobile species are highly isolated by a potentially hostile agricultural landscape matrix with low quality, *e.g.* homogeneous, structurally poor and low in complementary resources (Tscharntke *et al.* 2012). Among the major consequences of forest fragmentation are the pervasive loss of species and the related decrease in overall biodiversity (Fahrig 2003, Tscharntke *et al.* 2012). More recently, studies revealed that a loss in species diversity often entails a simultaneous loss in functional diversity, *i.e.* diversity of ecological functions that species perform *via* trophic interactions within their ecosystem (Rosenfeld 2002). Alarmingly, effects of forest fragmentation have been suggested to extend beyond bitrophic interactions and cause trophic cascades across multiple trophic levels thereby, altering properties of complex trophic networks (Schmitz *et al.* 2000, Halaj & Wise 2001, Knight *et al.* 2005). As a consequence, forest fragmentation may impair ecosystem functioning and eventually, pose a threat to ecosystem stability and vital ecosystem services (Bengtsson *et al.* 2000, Sala *et al.* 2000, Tscharntke *et al.* 2012, Martinson & Fagan 2014). A number of ecosystem services are highly specific to forest ecosystems and largely benefit human well-being, *i.e.* forests function as global carbon sinks, contribute to climate regulation and reduce the risk of erosion (Chapin *et al.* 2000, Sala *et al.* 2000, Ciccarese *et al.* 2012). Altogether, the necessity to maintain overall biodiversity and unconfined ecosystem functioning as well as the ubiquitous significance of forests for ecosystem services illustrate the need to address and evaluate the implications of forest fragmentation. With this thesis I aimed to investigate the impact of forest fragmentation on plant-herbivore interactions as insect herbivory is an important ecological process and shifts in insect herbviore communities may significantly alter forest ecosystems (Marquis 2004).

Plant-herbivore interactions in fragmented forests

Insects make up the vast majority of species worldwide, constitute a highly diverse group of organisms and are considered the most important organisms in terms of ecological functioning (Wilson 1992, Weisser & Siemann 2004, Schowalter 2006). Herbivorous insects are known to play a key role in all plant-based ecosystems (Marquis 2004). Despite their inconspicuousness compared to vertebrate herbivores, insect herbivores have profound effects on plants. By feeding on plants, insect herbivores affect growth, fitness and reproduction of plant individuals (Marquis 2004, Maron & Crone 2006, Schowalter 2006). Moreover, it has been suggested that effects of insect herbivory comprise long-term effects on plant species persistence as well as the structure and composition of plant-based ecosystems (Marquis 2004, 2005, Ruiz-Guerra *et al.* 2010).

Changes in insect herbivore communities due to forest fragmentation may involve severe consequences. Particularly, increased insect herbivore abundances may cause an overall increase in the susceptibility of plants to insect herbivory (Marquis 2004, Maron & Crone 2006). However, there is still no consensus on general effects of forest fragmentation on plant-herbivore interactions and the associated process of insect herbivory. So far, attempts to investigate plant-herbivore interactions in fragmented landscapes are underrepresented compared to mutualistic interactions and do not allow the drawing of reliable conclusions (Magrach *et al.* 2014). Moreover, previous studies that investigated plant-herbivore interactions in fragmented forests present conflicting results (Tscharntke & Brandl 2004, Magrach *et al.* 2014). In more detail, some findings indicate reduced insect herbivory in fragmented forests (Simonetti *et al.* 2007, Faveri *et al.* 2008, Ruiz-Guerra *et al.* 2010), whereas others suggest insect herbivory to increase with forest fragmentation (Rao *et al.* 2001, Barbaro *et al.* 2012) or not to be affected at all (Botzat *et al.* 2013). This discrepancy regarding the effect of forest fragmentation on plant-herbivore interactions and the associated process of insect herbivory may be a result of context-dependency (Chamberlain *et al.* 2014). Plant-herbivore interactions are embedded in

complex trophic networks and thus, insect herbivores are affected by their biotic environment, *i.e.* they respond to local patterns in host-plant availability and experience trophic top-down forces through predation (Chapin *et al.* 2000, Van Bael *et al.* 2003, Lewinsohn *et al.* 2005, Lewinsohn & Roslin 2008). Moreover, plant-herbivore interactions are dynamic and patterns in the performance of either partner of the interaction produce reciprocal changes of its counterpart (Paige & Whitham 1987, Karban & Baldwin 1997, Thompson 1999, Järemo *et al.* 2007). Hence, both context-dependency and the complex nature of antagonistic interactions may create spatial variability in plant-herbivore interactions (Järemo *et al.* 2007, Chamberlain *et al.* 2014). Hence, in order to draw reliable conclusions on potential shifts in plant-herbivore interactions and the related process of insect herbivory in fragmented forests it is necessary to simultaneously incorporate patterns of the local plant community (*i.e.* tree diversity), the ecological function of predators as well as potential feedback effects *via* plant responses to insect herbivory.

Interactive effects of forest fragmentation & tree diversity

In addition to forest fragmentation, the structure and composition of plant communities, *e.g.* the qualitative and quantitative availability of plant species, plays an important role for insect herbivores (Massey *et al.* 2006, Lewinsohn & Roslin 2008, Barbosa *et al.* 2009, Haddad *et al.* 2009). Interestingly, previous studies also found inconsistent responses of insect herbivores to patterns in plant communities. For instance, findings of studies imply that insect herbivory (or insect herbivore abundance as a surrogate) is higher in pure forest stands compared to mixed forest stands (Jactel & Brockerhoff 2007, Vehvilainen *et al.* 2007). This finding is in line with the *resource concentration hypothesis* (Root 1973) and the concept of *associational susceptibility* (or *associational resistance*; Brown & Ewel 1987). Both theories suggest that similar neighbouring plants facilitate the detection of a focal plant by herbivorous insects and thus, increase plant susceptibility to insect herbivory (White & Whitham 2000, Barbosa *et al.* 2009). In contrast, other studies suggest that levels of insect herbivory increase along with increasing tree species richness as higher host-plant diversity is assumed to sustain higher numbers of particularly generalist herbivorous insects (Vehvilainen *et al.* 2007, Unsicker *et al.* 2008, Schuldt *et al.* 2010). Despite the discrepancy in the aforementioned findings, studies largely agree that the effect of tree diversity may vary with the degree in host-tree specialization of herbivorous insects and depend on the identity of the focal host-tree species (Vehvilainen *et al.* 2007, Sobek *et al.* 2009). Consequently, community-level approaches with respect to both trophic levels – herbivorous insects as well as their host-plants – are essential to unravel effects of tree diversity on plant-herbivore interactions.

Studies aiming to explain the paradox of inconsistent responses to environmental drivers recently suggested that co-occurring environmental drivers interact and may therefore, create synergistic or antagonistic effects (Didham *et al.* 2007, de Sassi *et al.* 2012). Accordingly, consequences of one driver may strongly depend on the expression of another driver which makes it necessary to consider environmental drivers in concert (Didham *et al.* 2007, Tylianakis *et al.* 2008). Supporting the existence of interactive effects of environmental drivers, a recent study found increased species richness of generalist insect herbivores with increasing plant species richness, while the effect was more pronounced for connected grassland fragments compared to isolated fragments (Rösch *et al.* 2013). Similarly, forest fragmentation may mediate the effect of tree diversity (and *vice versa*), which may well explain the inconsistent responses of insect herbivores to both co-occurring environmental drivers. However, the validity of interactive effects of forest fragmentation and tree diversity as a source of inconsistent responses of herbivorous insects still needs empirical evidence, particularly as the drivers under consideration act on different spatial scales.

Ecological function of predators in fragmented forests

The trophic role of predators, particularly of insectivorous birds is ubiquitous (*e.g.* Greenberg *et al.* 2000, Van Bael *et al.* 2003, Şekercioğlu 2006, Mooney *et al.* 2010). The predation of insectivorous birds on insect herbivores reduces overall abundances of insect herbivores and thus, the degree of insect herbivory (Halaj & Wise 2001, Van Bael *et al.* 2003, Mooney *et al.* 2010, Böhm *et al.* 2011). Consequently, the trophic functioning of insectivorous birds benefits plant, *i.e.* in terms of biomass and reduced mortality, and is considered one of the most important ecosystem services (Chapin *et al.* 2000, Mäntylä *et al.* 2011).

While forest birds directly face the consequences of forest fragmentation, not all bird species

experience and respond to the associated landscape changes equally (Şekercioğlu *et al.* 2002). The susceptibility of species to environmental changes strongly depends on species-specific character traits, known as *environmental filtering* (Lebrija-Trejos *et al.* 2010, dos Santos *et al.* 2015, Kraft *et al.* 2015). It is particularly the preferences for certain forest habitat features, specialized food requirements as well as the vulnerability to forest edges and high-contrast landscape matrices, which determine the susceptibility of forest birds to forest fragmentation (Lindell *et al.* 2007, Vetter *et al.* 2011, Newbold *et al.* 2012). Based on the number of determinants it is difficult to predict the susceptibility of individual species to complex human-driven landscape modifications (Ewers & Didham 2006). However, recent studies suggest that insectivorous bird species may be highly susceptible to forest fragmentation and are at risk of disappearing from smaller forest remnants (Zanette *et al.* 2000, Şekercioğlu 2002, Şekercioğlu *et al.* 2002, Lindell *et al.* 2007, Kennedy *et al.* 2010, Newbold *et al.* 2012).

Initially, species with equivalent ecological functions like insectivorous birds were considered functionally redundant (Lawton & Brown 1994). Accordingly, the loss of species that are sensitive to disturbances was assumed to be compensated by more resistant species, which in turn, maintain the respective ecological function (Lawton & Brown 1994, Gonzalez & Loreau 2009). Hence, among insectivorous birds, the persistence of disturbance-resistant bird species may buffer the loss of disturbance-sensitive bird species and maintain the trophic control of insect herbivores. Based on this concept of functional redundancy, disturbances and the subsequent loss of certain species were believed to have little impact on ecosystem processes and ecosystem functioning (Rosenfeld 2002). There is however, no consensus regarding the generality of the concept of functional redundancy in real-world ecosystems (Fonseca & Ganade 2001, Davies *et al.* 2012). First, the respective species have to show high similarity in all species traits that characterise their ecological function but not in their susceptibility to forest fragmentation (Walker 1992). Moreover, the maintenance of ecological functioning requires full density compensation of the species that are lost (Rosenfeld 2002). Hence, it is unknown whether disturbance-resistant insectivorous birds maintain the ecological function or if a loss of insectivorous bird species due to forest fragmentation reduces species functioning and thus, disrupts trophic interactions (Hooper *et al.* 2005).

Alarmingly, a loss of insectivorous forest birds and their functioning would directly translate into a release of insect herbivores from predation pressure and thereby, cause increased insect herbivore abundances and ultimately, higher levels of insect herbivory (Barbaro *et al.* 2012, Ruiz-Guerra *et al.* 2012, De La Vega *et al.* 2012, Karp *et al.* 2013). However, whether forest fragmentation triggers cascading effects across multiple trophic levels with considerable consequences for forest ecosystems is unknown (Faveri *et al.* 2008, Karp *et al.* 2013, Maguire *et al.* 2015).

Feedback effects via plant responses to herbivory

During the process of herbivory, "the plant's shoot suddenly gets smaller because part of it walked off in the stomach of an herbivore" (Karban & Baldwin 1997, p. 90). Although this leaves the plant to deal with the consequences, ecological studies rarely addressed the plant's perspective as plants were perceived as inactive compared to their mobile trophic counterparts, *i.e.* insect herbivores (Karban & Baldwin 1997). However, plants are by no means unable to respond to impacts in their environment, *e.g.* the loss of photosynthetically active and thus, valuable leaf tissue due to insect herbivory. Predominantly, research in the field of plant physiology revealed that plants are able to tolerate insect herbivory and to defend themselves against insect herbivores. Plants trigger shifts in physiological processes such as the acquisition and allocation of resources and increase photosynthetic activity while experiencing insect herbivory (Karban & Baldwin 1997, Tiffin 2000, Nykänen & Koricheva 2004). In turn, higher growth rates enable the replacement of lost tissue, *i.e.* compensatory growth (Paige & Whitham 1987, Hawkes & Sullivan 2001). In addition, plants are able to induce the production of secondary metabolites that act as defence compounds and these have been suggested to deter insect herbivores from feeding (Karban & Baldwin 1997, Nykänen & Koricheva 2004). Consequently, compensatory growth enables plants to recover from insect herbivory while the induced defence has been suggested to create feedback effects on insect herbivores, *i.e.* affect the community composition and the performance of insect herbivores and in turn, the degree of insect herbivory on host-plants. Hence, plants possess the means to actively mediate plant-herbivore interactions and thus, "bringing the

plant back into plant-herbivore interactions" (Karban & Baldwin 1997, p. 100) is vital to capture the full complexity of the trophic interaction between insect herbivores and plants.

While plant responses to insect herbivory sound straightforward in theory, previous empirical studies showed that herbivory-induced changes in plant performance are variable and highly complex. For instance, plant responses to herbivory have been suggested to range from increased mortality rates to an "advantage of being eaten", *e.g.* beneficial overcompensation in terms of growth (Belsky 1986, Paige & Whitham 1987, Järemo *et al.* 2007). The source of this variation in plant responses may be manifold including species characteristics (*e.g.* growth rate; Coley *et al.* 1985, Massad 2013) and the extent of herbivory (*e.g.* intensity and frequency; Ferraro & Oesterheld 2002). Moreover, both mechanisms – compensatory growth and induced defence – are nutrient-demanding and thus, costly to the plant (Bryant *et al.* 1983, Coley *et al.* 1985, van der Meijden *et al.* 1988, Karban & Baldwin 1997). Both the nutrient dependency and the generally limited availability and heterogeneous distribution of nutrients have stirred the formulation of a hypothesized *growth-defence trade-off* after which plants favour either mechanism, particularly at high levels of herbivory and low nutrient availability (Coley *et al.* 1985, van der Meijden *et al.* 1988, de Jong & van der Meijden 2000, Endara & Coley 2011). However, there is still no consensus on effects of insect herbivory on plant growth and defence at different levels of nutrient availability. Thus, a comparative approach that synthesizes the outcomes of empirical studies in a statistical manner, accounts for the multitude of different plant species and incorporates the differences of experimental study conditions (*e.g.* intensity of herbivory) might be the next step towards understanding the complexity of plant responses elicited by insect herbivory.

Outline of the thesis

This thesis focuses on plant-herbivore interactions in forest ecosystems that face human-driven landscape modifications as a result of forest fragmentation. In particular, I aimed to explain the inconsistent responses of insect herbivores to forest fragmentation by addressing the context-dependency and the complex nature of antagonistic plant-herbivore interactions. I approached the above coherences by conducting two field studies in southern KwaZulu-Natal (South Africa) and by performing a comprehensive meta-analysis. Findings of this thesis shall provide a more holistic view on the underlying mechanisms that drive effects of forest fragmentation and thus, complement our current knowledge regarding shifts in plant-herbivore interactions and the associated process of insect herbivory in fragmented forests.

Study region

To unravel the context-dependency of plant-herbivore interactions in fragmented forests, I conducted two field studies in a subtropical forest landscape in South Africa. As a result of orographic conditions and palaeoclimatic changes, the forests in South Africa are confined to the eastern coast, predominantly the province of KwaZulu-Natal (Eeley *et al.* 1999, Mucina & Rutherford 2006). The study region is located near the southern coast of KwaZulu-Natal and characterized by a unique landscape of gorges and plateaus (Eeley *et al.* 1999), such as Oribi Gorge which is the centre of the study region. Presumably, Oribi Gorge was originally covered by tropical forest whereas today, the regional forest type is subtropical, evergreen scarp forest (Ezemvelo KZN Wildlife 2009). Scarp forests constitute a contemporary overlap zone of the Afrotemperate and the Indian Ocean Coastal Belt forest and thus, comprise a unique mixture of both forest types accompanied by high species diversity and species endemism (Eeley *et al.* 1999, Lawes *et al.* 2007, Ezemvelo KZN Wildlife 2009). As a result, scarp forests are considered to be the most valuable forest type in South Africa and thus, of high priority for biodiversity conservation (Eeley *et al.* 1999, Ezemvelo KZN Wildlife 2009). However, driven by the population growth of KwaZulu-Natal during the last 100 – 200 years, forest area has increasingly been converted, particularly into extensive sugar cane farming and, to a lesser extent, timber plantations and orchards (Eeley *et al.* 1999). As a result, the conversion of forests caused an overall loss in forest area and consequently, a patchy distribution of forest remnants on the plateaus, whereas the continuous forests are restricted to conservation areas and the gorges (*i.e.* Oribi Gorge; Ezemvelo KZN Wildlife 2009). Both the human-driven landscape modifications in KwaZulu-Natal and the conservation value of scarp forests in general, qualify this region for ecological studies on effects of deforestation and the related process of forest fragmentation on species diversity, multitrophic interactions and ecosystem functioning.

Meta-analyses in ecology

To address the complex nature of antagonistic plant-herbivore interactions, I performed a comprehensive meta-analysis. Meta-analyses combine the outcomes of similar empirical studies in a quantitative manner (as opposed to vote-counting; Combs *et al.* 2011) and thereby, make it possible to draw reliable conclusions regarding the heterogeneity and consistency of empirical findings (Hedges & Olkin 1985, Gurevitch & Hedges 1999, Combs *et al*. 2011). In more detail, a meta-analysis captures the outcome of a set of similar empirical studies by calculating an individual effect size per study that accounts for the statistical power of each study in terms of the size of the observed effect, the sampling variance and the sample size (Hedges & Olkin 1985). Subsequently, a meta-analysis summarizes the individual effect sizes of the empirical studies by calculating a mean effect size that includes information on the direction, the magnitude and the uncertainty or statistical variability of the overall effect (Hedges & Olkin 1985).

While meta-analyses originate from medical and social sciences, significant progress was made during the last decades in adapting meta-analyses to the field of biology, particularly ecology and evolution, *i.e.* with respect to the heterogeneity of experimental study designs and the phylogenetic relatedness among species (Chamberlain *et al.* 2012; Nakagawa & Santos 2012). The advances of ecological meta-analyses make them a powerful statistical tool to quantitatively synthesize and review complex ecological coherences.

Objectives

To unravel the context-dependency and complexity of antagonistic plant-herbivore interactions in fragmented forests, I conducted three consecutive studies that are presented in the following three chapters.

With the first field study (chapter 2), I addressed potential interactive effects of forest fragmentation on the landscape scale and local tree diversity on the community composition, species richness and the abundance of insect herbivores across a diverse array of host-plant species. Subsequently, I was interested whether forest fragmentation and potential shifts in community patterns of insect herbivores are linked to the ultimate degree of insect herbivory.

With the second field study (chapter 3), I aimed to unravel the effects of forest fragmentation on the community composition of birds and the ecological function of insectivorous birds. In particular, I was interested whether forest fragmentation causes a loss in the abundance of insectivorous birds and triggers a cascading effect across lower trophic levels, *i.e.* causes an increase in the abundance of insect herbivores and ultimately, higher insect herbivory.

Finally, by performing a comprehensive meta-analysis (chapter 4), I integrated the plant's perspective and the ability of plants to respond to herbivory and thus, mediate plant-herbivore interactions. In more detail, I investigated how herbivory affects the performance of plants in terms of compensatory growth and induced defence and whether patterns in the effects vary with respect to nutrient availability and experimental study conditions (*e.g.* intensity of herbivory). In this context, I further aimed to evaluate the validity of the hypothesized *growth-defence trade-off* in plants.

The three studies have been published in or have been submitted to scientific journals. The present background knowledge for the three studies is presented in the following three chapters and thus, the individual chapters two, three and four can be read independently.

Chapter 2

Effects of local tree diversity on herbivore communities diminish with increasing forest fragmentation on the landscape scale

with Franziska Peter, Dana G. Berens, Nina Farwig

a similar version of this manuscript has been published by *PLoS ONE*

Summary

Forest fragmentation and plant diversity have been shown to play a crucial role for herbivorous insects (herbivores, hereafter). In turn, herbivory-induced leaf area loss is known to have direct implications for plant growth and reproduction as well as long-term consequences for ecosystem functioning and forest regeneration. So far, previous studies determined diverging responses of herbivores to forest fragmentation and plant diversity. Those inconsistent results may be owed to complex interactive effects of both co-occurring environmental factors albeit they act on different spatial scales.

In this study, we investigated whether forest fragmentation on the landscape scale and tree diversity on the local habitat scale show interactive effects on the herbivore community and leaf area loss in subtropical forests in South Africa. We applied standardized beating samples and a community-based approach to estimate changes in herbivore community composition, herbivore abundance and the effective number of herbivore species on the tree species-level. We further monitored leaf area loss to link changes in the herbivore community to the associated process of herbivory.

Forest fragmentation and tree diversity interactively affected the herbivore community composition, mainly by a species turnover within the family of Curculionidae. Furthermore, herbivore abundance increased and the number of herbivore species decreased with increasing tree diversity in slightly fragmented forests whereas the effects diminished with increasing forest fragmentation. Surprisingly, leaf area loss was neither affected by forest fragmentation or tree diversity, nor by changes in the herbivore community.

Our study highlights the need to consider interactive effects of environmental changes across spatial scales in order to draw reliable conclusions for community and interaction patterns. Moreover, forest fragmentation seems to alter the effect of tree diversity on the herbivore community and thus, has the potential to jeopardize ecosystem functioning and forest regeneration.

Introduction

The interaction between herbivorous insects and their host-plants play a key role for forest ecosystems. By feeding on plants, herbivores determine growth, reproduction and survival of plants (Maron & Crone 2006). Thus, herbivory-induced leaf area loss (LAL) is considered an important factor for primary production, vegetation structure, the persistence of ecosystem functioning and regeneration of plant-dominated ecosystems like forests (Ruiz-Guerra *et al.* 2010). However, the ongoing conversion of forest area to agriculturally used land poses a major threat to indigenous forests, forest-associated species, their interactions and thus, the functioning of forest ecosystems (Sala *et al.* 2000).

Particularly, the increase of agriculturally used land at the expense of forest area results in small forest fragments that are spatially isolated by inhospitable landscape matrix (Fischer & Lindenmayer 2007). Thus, anthropogenically driven forest fragmentation leads to habitat loss and decreasing habitat connectivity with consequences for the availability and the spatial distribution of resources on the landscape scale (Tscharntke *et al.* 2012). As a result, forest fragmentation entails direct implications for the composition of local communities and species distribution on a landscape scale, thereby altering interactions and trophic network patterns (Tscharntke *et al.* 2012). Finally, forest fragmentation has been suggested to ultimately imperil ecosystem functioning and forest regeneration (Santo-Silva *et al.* 2013). Yet, recent research has revealed positive, negative and neutral responses of herbivores to forest fragmentation (Didham *et al.* 1998, Braschler *et al.* 2009, Ruiz-Guerra *et al.* 2010, Rösch *et al.* 2013) as well as diverging effects on LAL (Rao *et al.* 2001, Valladares *et al.* 2006).

In addition to forest fragmentation on the landscape scale, plant diversity on the local habitat scale has been shown to be equally important for herbivore communities (Barbosa *et al.* 2009). Plant diversity determines the number of different host-plant species as well as their proportionate availability. However, similarly to effects of forest fragmentation, studies showed diverging effects of tree diversity in forest habitats on herbivores as well as LAL (Jactel & Brockerhoff 2007, Vehvilainen *et al.* 2007, Haddad *et al.* 2009, Schuldt *et al.* 2010, Giffard *et al.* 2012).

The inconsistencies in the effects of forest fragmentation and tree diversity on herbivores and LAL may be caused by interactive effects. Recent studies showed that environmental changes may not only act additively but also synergistically or antagonistically, leading to either an amplification or attenuation of the individual effects (Didham *et al.* 2007, de Sassi *et al.* 2012). As a result, the emerging effect cannot be interpreted by separately focussing on single factors or by adding together

the individual effects (Didham *et al.* 2007). Thus, de Sassi *et al.* (2012) emphasize the need to consider both main effects and interactive effects of multiple, relevant, co-occurring factors in concert. Assuming interactive effects of forest fragmentation on the landscape scale and tree diversity on the local habitat scale may well explain the diverging responses of herbivores and LAL throughout the body of studies. For instance, a recent study of Rösch *et al.* (2013) showed an interactive effect of habitat isolation and plant species richness on a generalist leafhopper community. In this study, species richness of generalist leafhoppers increased with increasing plant species richness while the magnitude of the positive effect was higher in connected compared to isolated grassland habitats. Hence, forest fragmentation on the landscape scale and tree diversity on the local habitat scale may interact in a synergistic or antagonistic manner. Consequently, the direction and magnitude of the emerging effect of forest fragmentation and tree diversity on the herbivore community and on LAL may vary considerably. Yet, interactive effects of environmental changes that act on different spatial scales are still poorly understood. Moreover, it is unknown whether interactive effects of forest fragmentation and tree diversity show a consistent pattern for the entire herbivore community.

Therefore, the aim of our study was to investigate the interactive effects of forest fragmentation on the landscape scale and tree diversity on the local habitat scale on herbivore communities and on LAL. Since previous studies reported inconsistent results regarding effects of the two environmental factors we did not corroborate hypotheses regarding the character of the main effects of forest fragmentation and tree diversity. Yet, similarly to the study of Rösch *et al.* (2013) we hypothesized a change in the effect of tree diversity on the herbivore community along the gradient of forest fragmentation. Furthermore, depending on the direction and magnitude of the emerging interactive effect of forest fragmentation and tree diversity on the herbivore community, we expected LAL to change correspondingly.

Methods

Study region

The study was conducted within and around the Oribi Gorge Nature Reserve (OGNR; 30°40' to 30°45' S and 30°10' to 30°18' E; 1881 ha) in southern KwaZulu-Natal, eastern South Africa. The necessary research permits for the OGNR were obtained from Ezemvelo KZN Wildlife. All study sites outside OGNR were on private property of local farmers, who granted us access to their land. The average rainfall of the region ranges from 570 to 1625 mm per year with a maximum in summer (October to March) and the average daily temperature ranges from 13 to 23 °C (Ezemvelo KZN Wildlife 2009). The study region is characterized by a large proportion of agriculturally used land mainly comprising sugar cane. This agricultural landscape matrix is interspersed with indigenous forest, predominantly forest remnants and only a small number of continuous forests. The regional indigenous forest type is scarp forest constituting a mixture of Afrotemperate and Indian Ocean coastal belt forest (Lawes *et al.* 2007).

Forest fragmentation & tree diversity

Forest fragmentation on the landscape scale entails several consequences such as the loss of forest area, decreasing fragment size, and increasing isolation of forest remnants (Fahrig 2003). Studies assessing effects of spatial changes on the landscape scale determined the area of the respective land-use or habitat type within a given landscape to be the most important determinant for the composition and structure of biotic communities (Fahrig 2003, Tischendorf *et al.* 2003). Therefore, we defined forest fragmentation as the ratio of agriculturally used area to the total area within a given landscape. We selected ten study sites within continuous and fragmented indigenous scarp forests that showed an increasing degree of forest fragmentation within 1000 m radii around the centres of the study sites. We are aware that the response of herbivores to landscape changes is scale-dependent (Tischendorf *et al.* 2003). However, we chose the 1000 m radius as landscape effects on herbivores and herbivory have been shown to be strongest on a spatial scale between 500 and 1500 m (Thies *et al.* 2003). Furthermore, forest fragmentation for the 1000 m radius was highly correlated with forest fragmentation for other radii (500 - 1500 m; Pearson correlation: $r > 0.96$; $n = 10$; P-value < 0.001 in all cases), and the choice of the 1000 m radius should therefore not substantially influence our findings. Across the ten study sites forest fragmentation ranged from 0.08 to 0.87. Mean pair-wise distances between study sites ranged from 1,400 to 20,700 m (9,500 ± 5,400 m; mean ± standard deviation (SD) throughout). Calculations of forest fragmentation were based on KwaZulu-Natal Land Cover data from Ezemvelo KZN Wildlife (Ezemvelo KZN Wildlife 2011; resolution: 20 m * 20 m) using ArcGIS (9.3.).

On the local habitat scale we defined tree

diversity as the index of Shannon diversity. To asses tree diversity we randomly chose five plots (10 m * 10 m each) within each forest study site adding up to a total area of 500 m² per study site. The distances among plots and between the plots and forest edges were at least 10 m. Within the plots we identified all trees (Boon 2010) higher than 2 m and calculated tree diversity per study site. In total, we recorded 2,519 tree individuals from 147 tree species and 53 plant families. Species from the family Rubiaceae were most common (16.4%; 20 species), followed by species of Euphorbiaceae (12.8%; 9 species) and Sapotaceae (9.5%; 2 species). Tree diversity ranged from 1.72 to 3.22 comprising 17 to 48 different tree species. Forest fragmentation and tree diversity showed moderate but non-significant correlation (Pearson correlation: r = -0.50; n = 10; *P*-value = 0.138). We ultimately evaluated the potential collinearity and related goodness of our statistical results by calculating the Variance Inflation Factor (VIF) for the regression models (Smith, Koper, Francis, & Fahrig, 2009; see statistical analyses for details).

Choice of tree species & sampling of herbivores

To assess plant-herbivore interactions for a representative set of the tree community and the associated herbivore communities we selected the most abundant tree species per study site (focal tree species, hereafter). Thus, the selection was based on the availability of tree species at individual study sites. We included every tree species of which we found 15 individuals per study site within a range of about 50 m * 50 m. Across the ten study sites we selected 67 focal trees with 29 different tree species from 21 families (Appendix 2). The number of focal tree species ranged from five to nine tree species per study site and accounted for 47 to 78% of the tree community per study site (63 ± 10%). Due to differences in the abundance distribution of tree species within the study sites the composition of the set of focal tree species varied across the study sites. In order to account for the variation in tree species identity, we included a phylogenetic eigenvector into our statistical analysis.

For the collection of herbivores we applied standardized beating samples from the end of March to the middle of April 2012. To ensure the collection of sufficient numbers of herbivores we collected beating samples from 15 individuals per focal tree species per study site and pooled these samples for further analyses. The height of the selected tree individuals ranged from 2 to 3 m. The standardized beating technique involved ten beatings with a wooden club against one randomly selected part of the tree. We collected the beating samples in a plastic funnel connected to a water-filled container. We separated the insects from unintended by-catch and debris and stored them in small flasks (containing 70% ethanol). We identified the insects to the lowest taxonomic level possible (mainly family and genus level; Scholtz & Holm 2008) and further discriminated them into morphospecies. Literature and expert knowledge for species taxonomy was relatively coarse. However, as the taxonomic resolution is equal across the insect orders of our beating samples and study sites, the coarse taxonomic resolution should not affect our results. Finally, we determined the morphospecies that are herbivorous (including omnivorous families within Coleoptera). The relative abundance of herbivorous insects ranged from 0 to 80% per focal tree species per study site (27.6 ± 17.6%). For further analyses we only considered herbivorous insects.

Herbivore community composition, herbivore abundance & number of herbivore species

To analyse changes in the herbivore community composition due to forest fragmentation and tree diversity we compiled a matrix with abundances of herbivores per focal tree species per study site and applied a Hellinger-transformation. Based on the transformed abundance matrix we established a dissimilarity matrix by calculating Bray-Curtis distances. In addition to forest fragmentation and tree diversity, we included a spatial component to account for spatial autocorrelation of the occurrence of herbivore species (Thies *et al.* 2003). We derived the spatial component by applying a Principal Coordinates of Neighbourhood Matrix analysis (PCNM) on the abundance matrix. From a matrix of spatial eigenvectors we selected the most significant eigenvector by using stepwise forward selection with alpha = 0.01 and 9,999 permutations (PCNM1: adj. R^2 = 0.04; *P*-value = 0.001).

The abundance and the diversity of herbivores have been suggested to affect the feeding pressure per plant individual (Tylianakis *et al.* 2010). Thus, using the abundance matrix of herbivore species per tree species per study site we calculated herbivore abundance and the effective number of herbivore species (exponent of Shannon diversity; number of herbivore species, hereafter). We calculated the two response variables on tree species-level (*i.e.* for

each focal tree species per study site) to account for diverging responses of herbivores to the identity of focal tree species.

Estimation of leaf area loss

Leaf area loss (LAL) was defined as the percentage of lost photosynthetically active leaf area due to leaf-chewing. As our herbivore samples contained no leaf-mining larvae we assumed the completion of the larval stage of most leaf-mining insects, and thus, excluded LAL due to leaf-mining. We visually estimated LAL in the field for 30 randomly chosen leaves of ten tree individuals per focal tree species within each study site and calculated the mean percentage per tree species per study site.

Statistical analysis

To analyse effects of the spatial component, forest fragmentation, and tree diversity on the herbivore community composition we performed non-parametric permutational Multivariate Analysis of Variance (perMANOVA; Anderson 2001) using the transformed abundance matrix. The perMANOVA partitions dissimilarities across the chosen terms of predictor variables, here the spatial component, forest fragmentation and tree diversity. This analysis uses permutations on raw data within a specified group to evaluate significances of the predictors. In a perMANOVA the respective predictor variables are evaluated sequentially as determined by the formula interface and thus, significances may change depending on the order of terms in the model formula. Therefore, we fitted four separate models, shuffled the last predictor term in the model formula and took the statistics from the predictor variable of the last term.

To explore the causal relationships between forest fragmentation, tree diversity, herbivore abundance, number of herbivore species and LAL we conducted a path analysis. Accounting for the nested structure of our data we applied path analysis after Shipley's d-separation method (Shipley 2009) and used linear mixed-effects models (LMER). As random effects we assigned either, both, study site and focal tree species identity, or only the former as random effects depending on their individual values of explained variance for the respective models. To enable the comparison of the effect sizes of the fixed effects we applied z-transformation. The estimate of tree diversity for one study site constituted an outlier. Yet, removing the outlier did not change the results, and thus, we retained data points belonging to this study site. To ensure normal distribution of response variables we applied ln-transformation throughout. We fitted the LMERs using restricted maximum likelihood (REML) and derived the *P*-values from Markov Chain Monte Carlo sampling (*pMCMC*).

Following Shipley's path analysis we compiled a set of initial models based on the causal relationships between forest fragmentation, tree diversity, herbivore abundance, number of herbivore species and LAL (Fig. 1). The first model included the effect of forest fragmentation and tree diversity on their combined interactive term. The following two models included the main effects and interactive effects of forest fragmentation and tree diversity on herbivore abundance and the number of herbivore species. To account for the potential causal relationship between herbivore abundance and the effective number of herbivore species we additionally included herbivore abundance as predictor for the number of herbivore species in the latter model. The fourth model included the main effects and interactive effect of forest fragmentation and tree diversity, as well as the effects of herbivore abundance and the number of herbivore species on LAL.

To evaluate the potential collinearity of the two fixed effects forest fragmentation and tree diversity and the related goodness of our results we calculated the Variance Inflation Factor (VIF) for the models investigating the effects on herbivore abundance, number of herbivore species and LAL. The VIF represents the overall correlation of each predictor with all others in the same model (Smith *et al.* 2009). Generally, a VIF above 10 indicates "severe" collinearity while values below 4 have been suggested to be uncritical. The VIF values for all models were below the critical threshold (herbivore abundance: < 1.6; number of herbivore species: < 1.5; LAL: < 1.8). Thus, we are confident that the potential collinearity of forest fragmentation and tree diversity did not affect the results of our study.

Based on the significances we derived from the initial four models, we subsequently applied d-separation to test each hypothesized conditional independency separately using the LMERs. We thus obtained the probability that the partial slope of the dependent variable was significantly different from zero. Finally, we combined and tested the probabilities of all independence claims using C-Statistics (Shipley 2009). The result of the Chi^2-test supported the causal model assumptions ($C = 7.27$; $df = 16$; P-value = 0.968).

In order to account for the different sets of focal tree species across our study sites, we included a phylogenetic eigenvector in our analyses. We derived

the phylogenetic eigenvector by firstly generating a phylogenetic tree including all the tree species we sampled during the vegetation monitoring. We generated the phylogenetic tree using Phylomatic version 3 (http://phylodiversity.net/phylomatic/) based on a megatree (R20120829) provided by the online program. Using the application Phylocom version 4.2 and the internal megatree of the program with given branch lengths (based on the divergence in DNA sequence data; Wikström, Savolainen & Chase 2001) we adjusted the branch lengths of our phylogenetic tree. Based on this adjusted phylogenetic tree we calculated pairwise phylogenetic distances between all the tree species and compiled a distance matrix including the focal tree species per study site (in rows) and the phylogenetic distances to the rest of the focal tree species (in columns). Next, we applied a Principal Coordinates of Neighbourhood Matrix analysis (PCNM) on this distance matrix to generate a matrix of eigenvectors. With stepwise forward selection with alpha = 0.05 and 9,999 permutations, we selected one phylogenetic eigenvector for the individual response variables herbivore community composition, herbivore abundance, number of herbivore species and LAL. However, the individual phylogenetic eigenvectors had no effect on the tested response variables throughout (*pMCMC* > 0.095). Thus, we concluded that the identity of the chosen focal trees did not affect our results.

All statistical analyses were done using Software R version 2.14.2 (R Core Team 2015) including packages 'vegan' (Oksanen *et al.* 2013) for calculation of the number of herbivore species and the perMANOVA, 'packfor' (Dray *et al.* 2013) for forward selection, 'lme4' (Bates *et al.* 2014) for calculating LMERs and 'languageR' (Baayen 2011) for extracting *pMCMC*-values and plotting the interactive effects of LMERs.

Results

Herbivore community composition, herbivore abundance & number of herbivore species

Across the study sites we sampled 763 herbivorous insects (87 morphospecies) from seven orders with Coleoptera being most abundant (83.6%; Curculionidae 70.8%), followed by Orthoptera (10.6%), Blattodea (2.5%), Hemiptera (2.0%), Hymenoptera (0.8%), Diptera and Phasmatodea (0.3% each).

Herbivore community composition per tree species per study site was related to the spatial component ($R^2 = 0.04$; $F_{1,62} = 3.42$; *P*-value = 0.006; Fig. 2) and changed along the gradient of forest fragmentation ($R^2 = 0.06$; $F_{1,62} = 4.44$; *P*-value = 0.043), but was not affected by tree diversity ($R^2 = 0.04$; $F_{1,62} = 3.02$; *P*-value = 0.895). However, forest fragmentation and tree diversity interactively affected herbivore community composition per

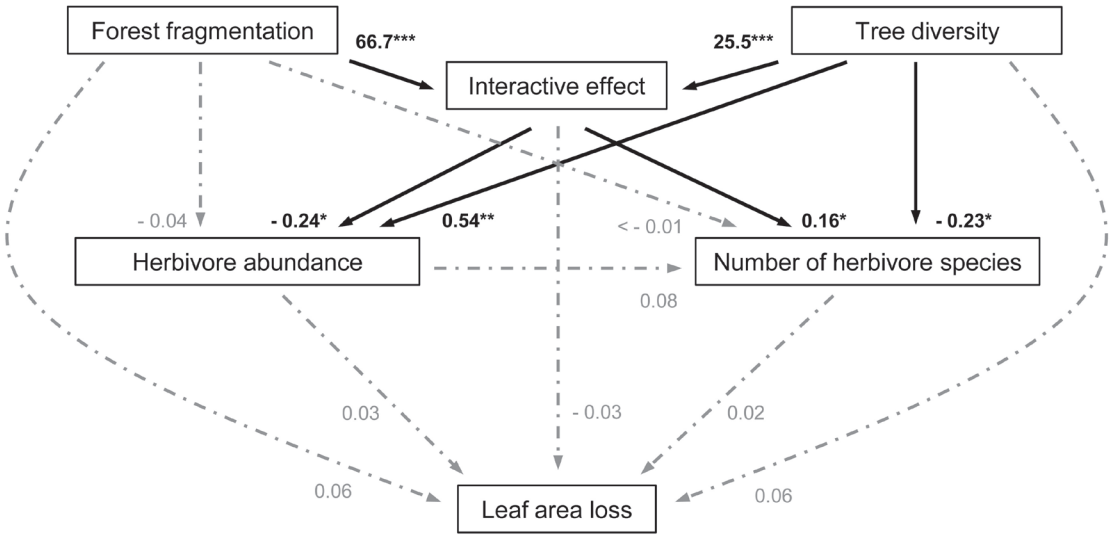

Figure 1: Path model for relationships between forest fragmentation, tree diversity, herbivore community, and leaf area loss.

Causal relationships between forest fragmentation, tree diversity, herbivore abundance, number of herbivore species, and leaf area loss; values next to arrows give effect estimates; black estimates and solid arrows show significant effects and stars demark the significance level (*pMCMC*: 0.050 < * > 0.010 < ** > 0.001 < *** > 0.000).

tree species per study site (R^2 = 0.05; $F_{1,62}$ = 4.14; *P*-value = 0.005). The observed changes were mainly driven by four species of the family Curculionidae (Coleoptera) that dominated the herbivore community throughout (58.5 ± 31.4% per tree species per study site). Interestingly, though abundances of Curculionidae were comparably high across all study sites, different species dominated the respective herbivore communities per tree species per study site.

Herbivore abundance per tree species ranged from 1 to 49 (11.4 ± 10.6; n = 67). Forest fragmentation did not affect herbivore abundance (Fig. 1). However, herbivore abundance increased with increasing tree diversity. Furthermore, forest fragmentation and tree diversity had an interactive effect on herbivore abundance (Fig. 3). Herbivore abundance only increased with increasing tree diversity in slightly fragmented forests whereas the effect diminished with increasing forest fragmentation. As herbivore abundance was not correlated with the number of tree individuals per study site we were able to exclude changes in herbivore abundance as a result of changes in the number of tree individuals (Pearson correlation: r = 0.04; n = 67; *P*-value = 0.741).

The number of herbivore species per tree species ranged from 1.0 to 7.5 (3.2 ± 1.7; n = 67). Forest fragmentation did not affect the number of herbivore species per tree species (Fig. 1). In contrast, the number of herbivore species per tree species

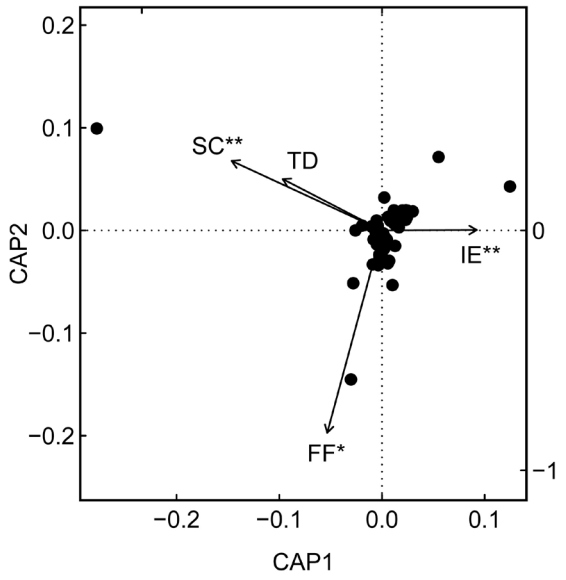

Figure 2: Effects of forest fragmentation and tree diversity on the community composition of herbivores.

Ordination plot of herbivore species per tree species per study site along the spatial component (SC), the gradients of forest fragmentation (FF) and tree diversity (TD) and their interactive effect (IE). Black points display species scores (n = 87) and stars demark the significance level (*pMCMC*: 0.050 < * > 0.010 < ** > 0.001 < *** > 0.000). We used a Constrained Analysis of Principal Coordinates (CAP) for visualization only as Software R does not provide a function to plot results of the perMANOVA.

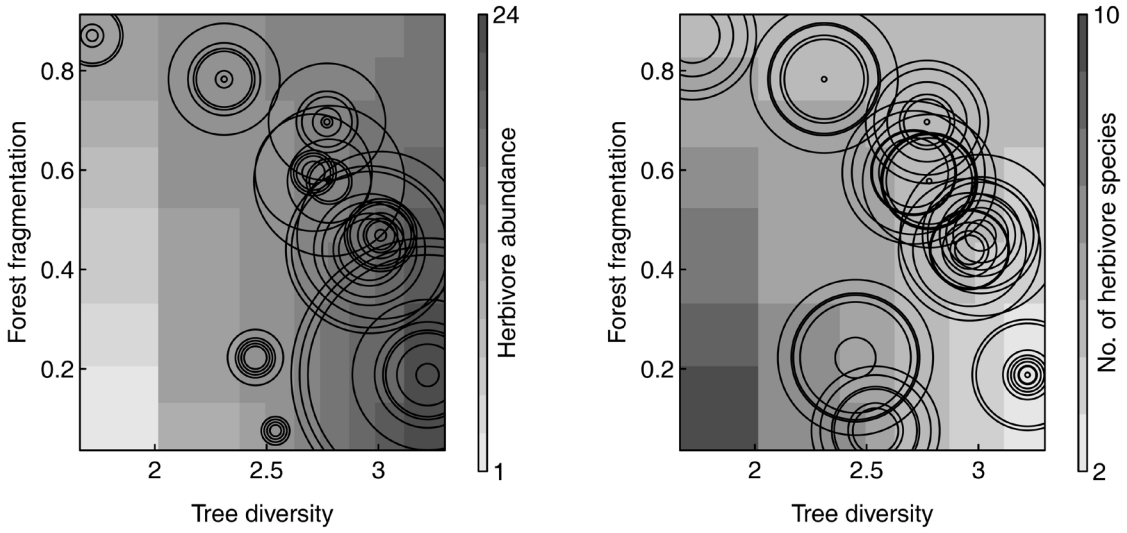

Figure 3: Effects of forest fragmentation and tree diversity on herbivore abundance and number of herbivore species.

Light to dark grey shaded areas depict low to high values for (left panel) herbivore abundance and (right panel) number of herbivore species per tree species per study site based on model fit; small to large radii of circles depict low to high values of original data for herbivore abundance and number of herbivore species per tree species per study site.

significantly decreased with increasing tree diversity. Yet, similarly to the interactive effect on herbivore abundance, the effect of tree diversity on the number of herbivore species was only present in slightly fragmented forests (Fig. 3). Furthermore, herbivore abundance and the number of herbivore species were not related to each other (Fig. 1).

Leaf area loss

LAL per tree species due to leaf chewing ranged from 0.7 to 26.0% (7.9 ± 0.7%; n = 67). Forest fragmentation and tree diversity had no main or interactive effects on LAL (Fig. 1). Furthermore, neither herbivore abundance nor the number of herbivore species per tree species per study site affected LAL per tree species.

Discussion

The results of our study showed that the community composition of herbivores changed due to interactive effects of forest fragmentation and tree diversity. Moreover, our results indicated an increase in herbivore abundance and a decrease in the number of herbivore species with increasing tree diversity for slightly fragmented forests. In contrast, in highly fragmented forests neither herbivore abundances nor the number of herbivore species changed along the gradient of tree diversity. Yet, despite the effects of forest fragmentation and tree diversity on herbivore abundance and the number of herbivore species we could not detect a link to LAL.

Main and interactive effects of forest fragmentation & tree diversity

The emerging pattern of the effects of forest fragmentation on the landscape scale and of tree diversity on the local habitat scale revealed two key aspects why studies need to consider interactive effects of environmental changes. Firstly, both forest fragmentation and tree diversity did not always show main effects on the herbivore community despite significant interactive effects. Thus, the effect of forest fragmentation and tree diversity on the herbivore community only became apparent through the interactive effects of both environmental factors. Furthermore, even after removing the interactive term from the model regressions the main effects did not become significant. Hence, if studies do not incorporate potential interactive effects of environmental changes they may be prone to overlook individual effects and draw wrong conclusions regarding their ecological significance (de Sassi *et al.* 2012). Secondly, while herbivore abundance and the number of herbivore species were affected by increasing tree diversity in slightly fragmented forests, both response variables did not change along the gradient of tree diversity in highly fragmented forests. Hence, the direction and the magnitude of the effect of one environmental factor may strongly depend on the specification of other environmental factors. Thus, according to our expectations our findings support that studies showing diverging responses of herbivores to changes in either forest fragmentation on the landscape scale or tree diversity on the local habitat scale may be biased by not accounting for potential interactive effects.

Herbivore community composition, herbivore abundance & number of herbivore species

The spatial component, forest fragmentation and tree diversity significantly affected the community composition of herbivores (Fig. 2). The Curculionidae, which accounted for the majority of herbivores, were highly abundant across all study sites. However, results indicated a species turnover within this family with forest fragmentation and tree diversity. The emerging pattern in the species turnover of herbivore communities along the gradient of forest fragmentation suggests a selection according to body size (measured as dry weight) and thus, dispersal ability. More specifically, Curculionidae showed specific shifts in body size with forest fragmentation: The mean dry weight of Curculionidae per tree species per study site ranged from 0.1 to 2.6 mg (0.8 ± 0.6 mg) and increased with increasing forest fragmentation (*pMCMC* = 0.014; estimate = 0.04). Thus, species that dominated the herbivore community in slightly fragmented forests were smaller and were gradually substituted by larger species with increasing forest fragmentation (> 20-fold increase in dry weight). This positive relationship between forest fragmentation and body size is congruent with findings of other studies (*e.g.* Jelaska & Durbesic 2009) and may be explained by environmental filtering of the herbivore community based on species-specific dispersal abilities (Ewers & Didham 2006, Bonte *et al.* 2010). Dispersal ability is positively linked to body size (Jelaska & Durbesic 2009) and thus, particularly large species may show a higher capability to traverse inhospitable matrices between isolated forest fragments (Ewers & Didham 2006, Tscharntke *et al.* 2012). In contrast, smaller species may be more susceptible to forest fragmentation and experience a decline in migration and recolonization

events (Fahrig 2003) resulting in comparably small population sizes on the local habitat scale (Maser *et al.* 2007, Wamser *et al.* 2012, Fischer *et al.* 2013).

At the same time, the environmental filter of forest fragmentation for higher dispersal ability may explain the interactive effects of forest fragmentation and tree diversity on overall herbivore abundance and the number of herbivore species. While herbivore abundance increased with increasing tree diversity in slightly fragmented forests, this effect diminished with increasing forest fragmentation. Thus, similarly to findings of Rösch *et al.* (2013), the spatial isolation of herbivore communities in fragmented forests may have hampered an overall increase of herbivore abundances with increasing tree diversity due to lower migration and recolonization events. Analogous, the decrease in the number of herbivore species with increasing tree diversity was only apparent in slightly fragmented forests. Large and highly mobile herbivore species that show a low susceptibility to forest fragmentation on the landscape scale are unlikely to respond to differences in tree diversity on the local habitat scale (Holland *et al.* 2005). Thus, environmental filtering of the herbivore community by forest fragmentation on the landscape scale may have driven the species turnover related to body size and simultaneously, may have circumvented the effects of tree diversity on the local habitat scale on herbivore abundance and the number of herbivore species in highly fragmented forests.

In contrast to the underlying mechanism of the effect of forest fragmentation, the effect of tree diversity on the herbivore community may be explained by species-specific differences in host-tree preferences and diet breadth (Barbosa *et al.* 2009). Increased tree diversity has been suggested to provide a higher number of supplementary or even more appropriate host-tree species within close proximity (*e.g.* Giffard *et al.*, 2012). In turn, particularly generalist species may benefit from dispersing across the increased variety of different tree species (Giffard *et al.* 2012) in order to feed on their preferred host-tree species, to reduce niche overlap and competitive pressure or to locate enemy-free space (Barbosa *et al.* 2009). As a result, increased tree diversity may support higher abundances of particularly generalist species (Sobek *et al.* 2009). This assumption corresponds to our finding that Curculionidae species that were related to study sites with high tree diversity were highly abundant on all focal tree species. In contrast, Curculionidae species that were associated with study sites showing low to medium tree diversity were only present on a subset of focal tree species and were less abundant throughout. The dispersal of certain herbivore species across the tree community with increasing tree diversity and the related increase in their individual abundances may simultaneously explain the overall increase in herbivore abundance with increasing tree diversity. Moreover, this dispersal of certain herbivore species in highly diverse forests may have also caused the reduction in the number of herbivore species per focal tree species. Thus, our results suggest that increased tree diversity promotes higher abundances of particularly generalist herbivores and leads to lower numbers of herbivore species per tree species in slightly fragmented forests.

Leaf area loss

Despite the interactive effects of forest fragmentation and tree diversity on the herbivore community we could not detect a link to LAL. This discrepancy may be explained by two not mutually exclusive factors. Firstly, LAL due to leaf-chewing represents an accumulation of feeding events throughout the whole season while our arthropod sampling represented only a "snapshot" of the current state of the arthropod community during the entire season of herbivore activity (Ings *et al.* 2009). Yet, diverse subtropical forests encompass a huge variety of herbivore species with different patterns regarding their life cycle and related changes in their feeding habits (Berenbaum & Isman 1989) leading to population fluctuations and changes in host-tree choice during their ontogenetic development (Arun & Vijayan 2004, Mody *et al.* 2007, Unsicker *et al.* 2008). As a result, a turnover in the herbivore community composition throughout the whole season (Ings *et al.* 2009, da Silva *et al.* 2011) may have compromised the conclusion whether effects of forest fragmentation and tree diversity on the herbivore community translate into changes in LAL. Secondly, the communities of herbivores on the respective focal tree species may have contained a certain proportion of tourist species that did not necessarily feed on the individual tree species and thus, may not have contributed to the respective degree in LAL. Hence, future studies should incorporate seasonal changes of herbivore communities and ensure the trophic interaction between herbivores and the focal tree species to further evaluate the interactive effects of environmental changes on the landscape and the local habitat scale on LAL.

Conclusion

With the interactive effects of forest fragmentation

on the landscape scale and tree diversity on the local habitat scale on the herbivore community we highlight the importance to consider joint effects of environmental changes across different spatial scales in general. Strikingly, tree diversity determined patterns of the herbivore communities while the magnitude of the effect on the herbivore community was altered by the degree in forest fragmentation. Based on our data, we could not confirm whether changes in the herbivore community due to forest fragmentation and tree diversity translate into changes in leaf area loss. Yet, findings of our study provide evidence that environmental changes across spatial scales may have the potential to ultimately affect primary production, vegetation structure, the persistence of ecosystem functioning, and the regeneration of forests via altered plant-herbivore interactions.

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CHAPTER 3

Forest fragmentation drives the loss of insectivorous birds and an associated increase in herbivory

with Franziska Peter, Dana G. Berens, Graham R. H. Grieve, Nina Farwig

a similar version of this manuscript has been accepted for publication by *Biotropica*

Summary

Insectivorous birds are known to play a decisive role for the natural control of herbivorous insects. Thus, they enhance the growth, reproduction and survival of plant individuals and in the long-term benefit plant regeneration. However, particularly in the tropics forest fragmentation has been suggested to cause a loss of insectivorous birds. Yet, it is unclear whether this hampers the trophic control of herbivorous insects with potential consequences for plants.

Therefore, we investigated the effect of increasing forest fragmentation on tritrophic interactions between insectivorous birds, herbivorous insects and plants in a subtropical forest landscape, South Africa. We monitored the community composition of birds and estimated insectivorous bird abundances along a gradient of forest fragmentation. In the same sites, we installed bird exclosures on a common plant species (*Englerophytum natalense*) to assess effects of the trophic control of insectivorous birds on herbivorous insects and leaf area loss.

Forest fragmentation strongly shaped the functional composition of bird communities, particularly through a loss of forest-dependent insectivorous birds. Moreover, leaf area loss was higher within bird exclosures than on control branches and increased with increasing forest fragmentation on the control branches.

Altogether, forest fragmentation seems to hamper the trophic control of herbivorous insects by insectivorous birds through changes in the community composition. This, in turn, may interfere with tritrophic interactions and ecological processes. Thus, conservation efforts aiming at enhancing the natural control of herbivorous insects should focus on the maintenance of continuous indigenous forests that are well-connected to smaller forest fragments on the landscape scale.

Introduction

The ongoing expansion of agricultural land at the expense of forest habitats leads to forest fragmentation (Fahrig 2003, Fischer & Lindenmayer 2007). As a result, forest fragmentation causes a patchy distribution of small forest fragments highly isolated by hostile agricultural landscape matrix (Fahrig 2003). Consequently, the provisioning with and the accessibility of habitat resources (*e.g.* nesting sites) on the local habitat scale and in the surrounding landscape decreases (Tscharntke *et al.* 2012). Previous studies showed that landscape changes associated with forest fragmentation strongly alter the structure and composition of forest bird communities worldwide (Giraudo *et al.* 2008). More specifically, increasing forest fragmentation has been suggested to reduce local bird diversity as well as inter-patch movement of particularly gap-sensitive and forest-dependent bird species in the tropics and subtropics (Stouffer & Bierregaard 1995, Stouffer *et al.* 2006, Boscolo & Metzger 2011, Newbold *et al.* 2012).

Besides the mere loss of habitat resources, increasing forest fragmentation increases the proportion of forest edges and reduces the proportion of forest interior (Kennedy *et al.* 2010). This shift in the ratio of forest edges to forest interior may play a major role for bird species' responses to forest fragmentation (Banks-Leite *et al.* 2010, Barbaro *et al.* 2012). Firstly, an increase in the proportion of forest edges has been suggested to increase the probability of nest predation thereby reducing the reproductive success of birds (Stratford & Robinson 2005). Moreover, particularly in tropical forests a shift in the ratio of forest edges and forest interior may drive changes in the provisioning of preferred food resources. In detail, forest edges have been suggested to provide higher shares of fruits, seeds and nectar compared to forest interior (Rodewald *et al.* 2004). As a result, open-habitat species with generalist food preferences, *i.e.* omnivorous birds that feed on a mixture of fruits, seeds, nectar and insects, may benefit from forest fragmentation. In contrast, food resources of insectivorous birds (*e.g.* Coleoptera) have been suggested to be more abundant in forest interior due to differences in microclimatic conditions (Zanette *et al.* 2000, Şekercioğlu *et al.* 2002, Martinson & Fagan 2014, Rossetti *et al.* 2014). Hence, especially in the tropics and subtropics forest-dependent food specialists such as insectivorous birds may be highly susceptible to forest fragmentation (Zanette *et al.* 2000, Şekercioğlu 2002, Şekercioğlu *et al.* 2002, Lindell *et al.* 2007, Kennedy *et al.* 2010, Newbold *et al.* 2012). The high susceptibility of forest-dependent insectivorous birds to increasing forest fragmentation and related high extinction rates are supported by several long-term studies (Sigel *et al.* 2006, 2010, Stouffer *et al.* 2009, 2011).

Given that insectivorous birds play a vital role for the trophic control of herbivorous insects (Van Bael *et al.* 2003, Sekercioglu 2006), especially tropical forest fragmentation may have potential consequences for ecological processes as well as plant regeneration

(Maron & Crone 2006, Şekercioğlu 2006, Mäntylä *et al.* 2011). The loss of predators such as insectivorous birds has been suggested to trigger cascades through multiple lower trophic levels, *e.g.* to lead to a release of herbivorous insects from predation pressure and related increases in insect herbivore abundances (Halaj & Wise 2001). Accordingly, previous studies from tropical (Van Bael *et al.* 2003), temperate (Böhm *et al.* 2011) and global scales (Mooney *et al.* 2010) showed that a loss of insectivorous birds caused increased insect herbivore abundances as well as higher leaf area loss (LAL). Moreover, a comprehensive meta-analysis by Mäntylä and colleagues (2011) showed that birds ultimately benefit plants regarding higher plant biomass and reduced plant mortality. Therefore, forest fragmentation may hamper the trophic control of herbivorous insects by insectivorous birds and thus, interfere with tritrophic interactions between insectivorous birds, herbivorous insects and plants (Ruiz-Guerra *et al.* 2012). However, to our knowledge so far only Karp *et al.* (2013) investigated the complete tritrophic relationships between forest fragmentation, insectivorous birds, herbivorous insects and ultimately LAL within coffee plantations. In their study, a decrease in the amount of natural forest cover surrounding coffee plantations caused a loss of insectivorous birds and a simultaneous increase in the number of coffee berry borers and berry infestation rates. However, agroforestry systems such as coffee plantations are anthropogenically used and structurally modified habitats. While shaded agroforestry systems have been suggested to harbour levels of biodiversity comparable to indigenous forests the community composition of birds may greatly differ (Philpott *et al.* 2008, Tscharntke *et al.* 2011, Şekercioğlu 2012). Moreover, the maintenance of bird communities and related ecological processes in agroforestry systems may show a higher dependency on the availability of supplementary resources and on higher recolonization rates from the surrounding landscape than communities in indigenous forests (Landis *et al.* 2000, Schroth & Harvey 2007, Anand *et al.* 2008, Chang *et al.* 2013). Consequently, it is important to know whether effects of tropical forest fragmentation on the landscape scale show similar patterns for agroforestry systems and indigenous forests regarding the tritrophic interaction between insectivorous birds, herbivorous insects and plants (Halaj & Wise 2001).

The aim of our study was to investigate whether the fragmentation of indigenous forests significantly alters the community composition of birds, particularly through a loss in the abundance of insectivorous birds. Most importantly, we aimed at analyzing whether the fragmentation of indigenous forests may trigger cascades through tritrophic interactions beginning with a potential loss of insectivorous birds, followed by a subsequent increase in insect herbivore abundances and ultimately higher LAL.

METHODS

Study region

The study was carried out within and around the Oribi Gorge Nature Reserve (30°40' to 30°45' S and 30°10' to 30°18' E; 1881 ha) in southern KwaZulu-Natal, eastern South Africa. The average rainfall of the region ranges from 570 to 1625 mm per year with a maximum in summer (October to March) and the average daily temperature ranges from 13 to 23°C (Ezemvelo KZN Wildlife 2009). The study region is a landscape mosaic dominated by agriculturally used land (mainly sugar cane) and interspersed with indigenous forest. The regional indigenous forest type is scarp forest constituting a mixture of Afrotemperate and Indian Ocean coastal belt forest (Lawes *et al.* 2007). The patchy distribution of scarp forests is the result of natural fragmentation due to orographic and palaeoclimatic conditions (Eeley *et al.* 1999). However, the increasing expansion of agricultural land-use and rural settlements during the last 100 to 200 yr caused severe loss of forest area and further exacerbated the fragmentation of the remaining scarp forests (Eeley *et al.* 1999). Still, regional scarp forests have been suggested to play an important role for the conservation of forest-dependent birds (Brown 2006, Neuschulz *et al.* 2013).

Forest fragmentation & vegetation heterogeneity

We selected 15 study sites covering a gradient of forest fragmentation with mean pairwise distances between study sites ranging from 1,000 to 22,300 m (9,800 ± 5,300 m; mean ± SD, throughout). We defined forest fragmentation as perimeter to area ratio of scarp forest because it has been suggested that forest-dependent, insectivorous birds benefit from large areas of forest interior with a low proportion of forest edges (Şekercioğlu *et al.* 2002). While forest management (*e.g.* logging) has been suggested to be similarly important for bird communities we can exclude it as a driver as our study sites were not subject to any management activities (personal

observation). We calculated forest fragmentation as a landscape-level metric using FRAGSTATS version 4.0 (McGarigal *et al.* 2012) within 500 m radii around the centre of our study sites. Calculation of forest fragmentation was based on KwaZulu-Natal Land Cover data from Ezemvelo KZN Wildlife (2011) using ArcGIS version 9.3. We are aware that the response of birds to landscape changes is scale-dependent. However, previous studies showed that forest-dependent birds respond to landscape changes on a spatial scale between 200 and 500 m, while effects on larger spatial scales up to 10 km seem to be similar (Smith *et al.* 2011, Karp *et al.* 2013). Furthermore, our gradient of forest fragmentation for the 500 m radius was highly correlated with forest fragmentation for other radii (200 m, 700 m, 1000 m; Pearson correlation: $r > 0.96$; $n = 15$; *P*-value < 0.001 in all cases) and the choice of the 500 m radius should therefore not substantially influence our findings. The gradient of forest fragmentation ranged from 80 to 4,020 (1,220 ± 1,090; see Appendix 3.1 for exemplary study sites along an increasing gradient of forest fragmentation).

We assessed vegetation heterogeneity as the Shannon diversity of biomass cover in different heights to control for potential effects of structural complexity of the vegetation on the bird community (Bibby *et al.* 2000). We estimated the proportion of living biomass cover independently for different heights (0 m, 1 m, 2 m, 4 m, 8 m and 16 m above ground) within three randomly chosen circle plots per study site. We then calculated a mean Shannon diversity per study site combining the estimates of the different heights. The circle plots had a radius of 5 m and the centres of the circle plots had a minimum distance of 10 m. Vegetation heterogeneity ranged from 0.87 to 1.20 (1.04 ± 0.09). Forest fragmentation and vegetation heterogeneity were not correlated (Pearson correlation: $r = 0.22$; $n = 15$; *P*-value = 0.243).

Bird community & abundance of insectivores

To monitor the bird community we did bird point counts. Point counts were based on bird calls only due to the dense forest structure which restricted visibility (Bibby *et al.* 2000). All point counts were carried out by the same person (G. Grieve) who has more than 25 yr of experience for bird call identification in South African forests. In cases where bird identification was uncertain, bird calls were recorded and identification was confirmed later by playback. We did two monitoring sessions across all 15 study sites (late October and early December 2012; $n = 30$). We selected this particular time frame as it covers the peak of the breeding season which has been suggested to be highly related with increased bird call activity (Symes *et al.* 2002, Brown 2006). Thus, the choice of the breeding season enabled the monitoring of a large proportion and a representative set of the local bird community. During each monitoring session, we did three bird point counts per study site at different randomly chosen locations which were at least 60 m apart. For each point count we monitored birds within a radius of 30 m. Each point count had the duration of 15 minutes (total: (15 min * 3 points counts * 2 monitoring sessions)/ study site = 90 min/ study site). The locations for the bird monitoring were not necessarily identical with the locations we used to estimate vegetation heterogeneity as both approaches had to fulfil different criteria, *e.g.* area of interest around the centre points and thus, distance between the centre points. Point counts were carried out in up to three study sites per day within a short time frame from sunrise (varying between 0430h and 0500 h) to 0900 h and at similar weather conditions (medium temperatures, no wind and no rain). To account for temporal variation within the chosen time frame we shuffled the order of the study sites between the first and the second monitoring session. In general, bird point counts have been suggested to have a higher probability of double-counting of the same individual (Buckland *et al.* 2008). Thus, we only recorded more than one individual of the same species for each bird point count per study site when they were calling at the same time. To estimate species abundances we pooled our results from the three point counts per study site per monitoring session. Furthermore, we classified insectivorous birds as species whose diet contains considerable shares of insects. We defined insectivorous birds following the approach of Kissling *et al.* (2007) using keywords ("mainly", "(almost) entirely", "(almost) exclusively", "prefers") based on the description of food and feeding behaviour in Roberts Birds of Southern Africa (Hockey *et al.* 2005). Finally, we calculated the abundance of insectivorous birds per study site per monitoring session.

Focal tree species & bird exclosures

To assess the impact of the trophic control of insectivorous birds on herbivorous insects we installed bird exclosures on selected focal trees in all study sites. As focal tree species we chose *Englerophytum natalense* (Sapotaceae) as it is an

abundant tree species within the indigenous forests along the coast of eastern South Africa (Boon 2010, Peter *et al.* 2014). Moreover, *E. natalense* seemed appropriate with respect to the aim of our study as a previous study showed that abundances of leaf-chewing insects and leaf area loss for *E. natalense* are relatively high compared to other tree species of the regional scarp forests (Peter *et al.* 2014). *Englerophytum natalense* is a small to medium evergreen tree (< 10 m, rarely up to 20 m) with simple, narrowly elliptic leaves (5 – 16 cm * 2 – 5 cm) fed upon by leaf-chewing insects (van Wyk & van Wyk 1997, Boon 2010). Within each study site we selected five focal tree individuals and installed bird exclosures from the end of October to the end of December 2012. Focal tree individuals had a height of 2 to 3 m with a minimum number of 200 leaves each and a distance of at least 10 m from each other. On every focal tree individual we installed one bird exclosure covering a representative branch with 50 to 60 mature leaves. We used fabric dark green mesh nets (mesh size: 1 cm * 1 cm) for the bird exclosure. We installed and regularly adjusted the bird exclosures in a way that ensured unrestricted plant growth throughout the whole study period. The bird exclosures had irregular shapes due to the branch structure but covered an average volume of 0.1 - 0.2 m³ (lengths: 60 – 80 cm, widths and height: 40 – 50 cm). Altogether, owing to their inconspicuousness, we are confident that the bird exclosures did not affect the foraging behaviour of birds. At the same time, we marked an additional branch per focal tree individual comprising a similar number of mature leaves and assigned this branch as the control branch. The assignment of bird exclosure and control branch on the same tree individual had the following advantages: Firstly, both treatments were underlying the same microclimatic habitat conditions, *e.g.* resource availability or vegetation community and structure surrounding the focal plant. Secondly, the characteristics of the focal tree were the same for the two treatments, *e.g.* age, growth structure or history of insect herbivore attacks and related levels of secondary defence metabolites.

Insect herbivore abundance & leaf area loss

To investigate the effect of the bird exclosure on abundances of herbivorous insects we did standardized beating samples at the end of the study period. We took beating samples from both the bird exclosure and the control branch for every focal tree individual per study site. Subsequently, we pooled beating samples per treatment, *e.g.* bird exclosure or control branch per study site (n = 30). The standardized beating technique involved ten beatings with a wooden club against the branch of the focal tree. The installation of both bird exclosure and control branch on the same tree individual required careful handling of the branches during the application of beating samples to avoid disturbances of herbivorous insects on the other branch. Thus, during the beating sample of one branch the joint of the respective branch and a close part of the main stem were kept steady. Moreover, we randomly started with either beating samples on bird exclosure or control branch to avoid systematic errors. We collected the beating samples in a plastic funnel connected to a water-filled container. We separated the insects from unintended by-catch (*e.g.* predatory arthropods, such as Mantidae) and debris and stored them in small flasks (containing 70% ethanol). We identified the insects to the lowest taxonomic level possible (mainly genus level; Scholtz and Holm 2008) and further discriminated them into morphospecies. For further analyses we only considered species which are classified as leaf-chewing herbivores (Scholtz & Holm 2008).

Furthermore, we monitored the leaf area loss (LAL) at the end of the study period for both the bird exclosure and the control branch. The study period included the growth period of new leaves. The leaves were fast growing and in the end of the study it was not possible to distinguish between this year's leaves and leaves of previous years. Thus, the final number of leaves on the branches exceeded the number of leaves at the onset of the study (50 to 60 leaves per treatment branch). However, as the number of new grown leaves was similar across the study sites and treatments we are confident that leaf growth did not affect our results. We defined LAL as the percentage of lost photosynthetically active leaf area and visually estimated LAL in the field for all individual leaves (n = 12,373) on the chosen branches with a precision of 5 percent.

Statistical analyses

To investigate the effects of forest fragmentation and vegetation heterogeneity on the community composition of all sampled birds, we first compiled an abundance matrix of bird species per study site per monitoring session based on the bird point counts. Subsequently, we applied Hellinger-transformation on the abundance matrix. Based on the transformed abundance matrix we established a dissimilarity matrix by calculating Bray-Curtis distances.

We included a spatial component to account for potential spatial autocorrelation of the occurrence of bird species (Thies *et al.* 2003). We derived the spatial component by applying a Principal Coordinates of Neighbourhood Matrix analysis (PCNM) on the abundance matrix. From a matrix of spatial eigenvectors we selected all significant eigenvectors by using stepwise forward selection with alpha = 0.05 and 9,999 permutations (significant eigenvector: PCNM4 with adj. $R^2 = 0.05$; *P*-value = 0.043). To analyse effects of forest fragmentation, vegetation heterogeneity and the spatial component on the bird community composition we performed non-parametric permutational Multivariate Analysis of Variance (perMANOVA; Anderson 2001) using the transformed abundance matrix. The perMANOVA partitions dissimilarities across the chosen terms of predictor variables, here forest fragmentation (ln-transformed), vegetation heterogeneity and the spatial component. This analysis uses permutations on raw data within a specified group to evaluate significances of the predictors. In a perMANOVA the respective predictor variables are evaluated sequentially as determined by the formula interface and thus, significances may change depending on the order of terms in the model formula. Therefore, we fitted three separate models, shuffled the last predictor term in the model formula and took the statistics from the predictor variable of the last term (Type III SS).

To investigate the causal relationship between forest fragmentation (ln-transformed), vegetation heterogeneity and the abundance of insectivorous birds we calculated a linear mixed-effects model (LMER). Study site was treated as random effect and we fitted the LMER using restricted maximum likelihood (REML) and derived the P-values by applying a cf-test.

To investigate the causal relationships between forest fragmentation (ln-transformed), bird exclosure treatment, abundance of herbivorous insects (sqrt-transformed) and LAL we calculated two general linear mixed-effects models (GLMER) due to left skewed distribution of raw data of insect herbivore abundance and LAL. The first GLMER contained the effects of forest fragmentation, bird exclosure treatment and their interactive effect on the abundance of herbivorous insects. Study site was treated as random effect and we fitted the GLMER using poisson family for count data. The second GLMER contained the effects of forest fragmentation, bird exclosure treatment and their interactive effect on LAL. We converted percentages of LAL to a binomial distribution of 0 to 20 (due to 5% precision) incorporating both LAL and the remaining leaf area in the model formula. Data of LAL were nested in study site, tree individual and treatment. We fitted the GLMER using binomial family with logit-transformation on LAL.

All statistical analyses were done using Software R version 3.1.0 (R Core Team 2015) including packages 'vegan' (Oksanen *et al.* 2013) for the perMANOVA, 'packfor' (Dray *et al.* 2013) for forward selection, 'lme4' (Bates *et al.* 2014), 'multcomp' (Hothorn *et al.* 2008) and 'effects' (Fox 2003) for the LMER and GLMERs, respectively.

RESULTS

Bird community & abundance of insectivores

Altogether, we recorded 1,011 bird individuals from 68 different species (Appendix 3.2). Bird abundances were similar across the two sessions of bird monitoring in October and December 2012 (session 1: 514 individuals; session 2: 497 individuals). The most abundant bird species across the two sessions were the Cape White-eye (*Zosterops virens*: 70 individuals), the Dark-capped Bulbul (*Pycnonotus tricolor*: 66 individuals), the Green-backed Camaroptera (*Camaroptera brachyura*: 64 individuals), the Olive Sunbird (*Cyanomitra olivacea*: 60 individuals) and the Southern Boubou (*Laniarius ferrugineus*: 59 individuals). Out of the 68 bird species, 35 species were insectivorous and the remaining species were omnivorous (25 species) and frugivorous (8 species).

The community composition of birds showed a species turnover along the gradients of vegetation heterogeneity and forest fragmentation, whereas the spatial component showed no

Table 1: Effects of forest fragmentation and vegetation heterogeneity on the community composition of birds.

Results were derived from perMANOVA with bird point counts for 15 study sites with two monitoring sessions each (n = 30). Study site was treated as random effect. Significant effects (P-value < 0.05) highlighted in bold.

	R^2	$F_{(3,26)}$	*P*-value
Vegetation heterogeneity	0.07	2.21	0.005
Forest fragmentation	0.08	2.69	< 0.001
Spatial component	0.04	1.17	0.323

effect (Tab. 1; Fig. 1). For example, the Terrestrial Brownbul (*Phyllastrephus terrestris*, PhTe, Fig. 1) was more abundant in forests with complex and dense vegetation whereas the Fork-tailed Drongo (*Dicrurus adsimilis*, DiAd) seems to prefer forests habitats with lower vegetation heterogeneity. Moreover, open-habitat bird species that are omnivorous, such as the Dark-capped Bulbul (*Pycnonotus tricolor*, PyTr) and the Cape White-eye (*Zosterops virens*, ZoVi) were highly abundant in highly fragmented forests. On the contrary, particularly insectivorous birds with high dependence on large forest interior, such as the Black Cuckoo (*Cuculus clamosus*, CuCl) and the Terrestrial Brownbul (*Phyllastrephus terrestris*, PhTe) seemed to prefer lightly frag-mented forests. Frugivorous birds, predominantly comprising pigeon and dove species, centred on intermediate forest fragmentation.

The abundance of insectivorous birds ranged from 3 to 29 individuals per study site in the first session (16.3 ± 7.8; mean ± SD, throughout) and from 6 to 24 individuals per study site in the second session (15.3 ± 6.0). The abundance of insectivorous birds was not affected by vegetation heterogeneity but decreased significantly with increasing forest fragmentation (Tab. 2, Fig. 2a).

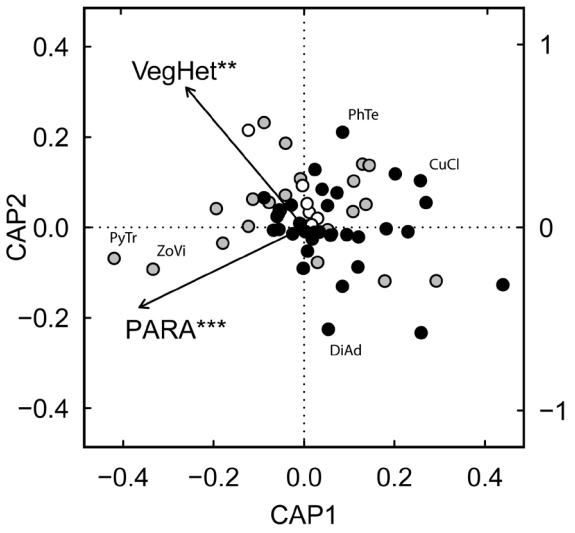

Figure 1: Effect of forest fragmentation and vegetation heterogeneity on the community composition of birds.

Points depict species scores (n = 68) for insectivorous (black; n = 35), omnivorous (grey; n = 25) and frugivorous bird species (white; n = 8); PARA = forest fragmentation and VegHet = vegetation heterogeneity; stars depict the significance level: 0.050 < * > 0.010 < ** > 0.001 < *** > 0.000; we used a Constrained Analysis of Principal Coordinates (CAP) for visualization only as Software R does not provide a function to plot results of the perMANOVA.

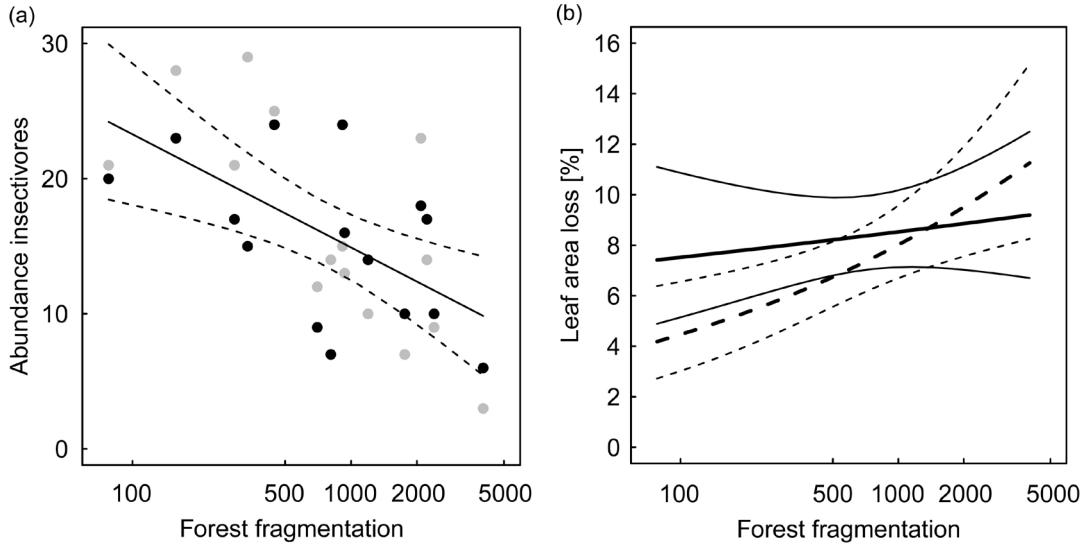

Figure 2: Effect of forest fragmentation on (a) the abundance of insectivorous birds and (b) leaf area loss (LAL).

(a) Points depict raw data of bird abundances of the 15 study sites for the first (grey) and the second (black) monitoring session (n = 30); the solid line depicts the LMER model fit and the dashed lines depict the 95% confidence interval; we treated study site as random effect. (b) The solid lines show the effect for the bird exclosure treatment and the dashed lines show the effect for the control branch; bold lines show the model fit and the thin lines show the 95% confidence intervals for the bird exclosure treatment and the control branch; leaf area loss per leaf was nested in study site, tree individual and treatment (n = 12,373).

Table 2: Effects on the abundance of insectivorous birds, abundance of herbivorous insects and leaf area loss (LAL).

Results were derived from LMER for the abundance of insectivorous birds and GLMERs for the abundance of herbivorous insects and LAL (see method section for details); treatment = control vs. bird exclosure; significant effects (*P*-value < 0.05) highlighted in bold.

	Abundance of insectivorous birds		**Abundance of herbivorous insects**		**LAL**	
	estimate	*P*-value	estimate	*P*-value	estimate	*P*-value
Vegetation heterogeneity	-9.06	0.670	--	--	--	--
Forest fragmentation	-5.31	**0.004**	-0.11	0.535	0.06	0.505
Treatment	--	--	2.04	0.097	1.52	**0.009**
Forest fragmentation * Treatment	--	--	-0.20	0.274	0.21	**0.016**

Insect herbivore abundance & leaf area loss

Altogether we sampled 188 arthropods (from 75 trees in total; 15 study sites * 5 trees) with 82 individuals being herbivorous insects. Therefore, insect herbivore abundances were admittedly low. The most abundant families were Apionidae (32.2%), Chrysomelidae (10.9%) and Curculionidae (10.9%; *see* Appendix 3.3 for a list of morphospecies). Insect herbivore abundance (pooled across five focal trees per study site) for the bird exclosures ranged between 0 to 12 herbivorous insects per study site (3.9 ± 3.8) and for the control branches between 0 to 7 insect herbivores per study site (1.5 ± 1.8). Leaf area loss (LAL) ranged from 0 to 80 percent per leaf for the bird exclosures (10.1 ± 24.0%) and from 0 to 90 percent per leaf for the control branches (8.9 ± 21.3%).

The abundance of herbivorous insects was neither affected by the main nor the interactive effect of forest fragmentation and the bird exclosure treatment (Tab. 2). In contrast, LAL was significantly higher on the bird exclosure branches compared to the control branches and increased with increasing forest fragmentation (Tab. 2; Fig. 2b).

DISCUSSION

The findings of our study suggest that forest fragmentation has an effect on the functional composition of bird communities as well as cascading effects through tritrophic networks. More specifically, forest fragmentation and vegetation heterogeneity shaped the community composition of birds. The effect of forest fragmentation on the community composition of birds was mainly driven by a decrease in the abundance of insectivorous birds. Results of the bird exclosure experiment showed no effect of forest fragmentation or bird exclosures on the abundance of herbivorous insects. Yet, leaf area loss (LAL) was higher within the bird exclosures compared to the control branches. Finally, LAL on the control branches increased with increasing forest fragmentation.

Community composition of birds & abundance of insectivores

A closer look at the community analysis suggests that the gradient of vegetation heterogeneity reflects the distinct preferences of bird species for certain structural features of the forest habitat such as closed canopy and dense understory vegetation. In contrast, the degree of forest fragmentation seems to mirror habitat requirements and food preferences of birds. This is in line with other studies that suggest the degree of forest dependency and species-specific resource requirements to be good predictors for bird species' responses to forest fragmentation (Kennedy *et al.* 2010, Neuschulz *et al.* 2011). Thus, our results indicate that open-habitat bird species that are omnivorous, such as the Dark-capped Bulbul (*Pycnonotus tricolor*, PyTr) and the Cape White-eye (*Zosterops virens*, ZoVi), may benefit from forest fragmentation. On the contrary, particularly insectivorous birds with high dependence on large forest interior, such as the Black Cuckoo (*Cuculus clamosus*, CuCl) and the Terrestrial Brownbul (*Phyllastrephus terrestris*, PhTe) seem to be negatively affected by changes in habitat and food availability caused by increasing forest fragmentation. The association of insectivorous birds with low forest fragmentation is in line with the significant decrease in the abundance of insectivorous birds (about 10-fold loss) from low to high forest fragmentation. Therefore, our results are congruent with findings of other studies suggesting a loss of particularly forest-dependent insectivorous

birds with forest fragmentation (Şekercioğlu 2002, Şekercioğlu *et al.* 2002, Stratford & Stouffer 2013, Sam *et al.* 2014). Considering the natural fragmentation of the scarp forests in our study system as a result of orographic and palaeoclimatic conditions one may expect a certain degree of adaptation to anthropogenic forest fragmentation (Neuschulz *et al.* 2013). Therefore, the strong effect of increasing forest fragmentation on the community composition of birds is an alarming signal for the conservation of species diversity and ecological processes. In turn, potentially less adapted bird communities may respond even stronger to increasing forest fragmentation.

Effect on the tritrophic interaction between insectivorous birds, herbivorous insects & plants

Changes in the community composition of birds associated with a decrease in the abundance of insectivorous birds, in turn, may mitigate the feeding pressure on herbivorous insects (Van Bael *et al.* 2003, Ruiz-Guerra *et al.* 2012). As we did not apply bird observations at our focal trees we cannot proof that insectivorous birds were actually feeding on insect herbivores on *E. natalense*. However, the majority of insectivorous birds in our study is known to forage within the vegetation and glean insects from trees (Appendix 3.2) and thus, the overall abundance of insectivorous birds was highly correlated with the abundance of gleaning insectivorous birds (Pearson correlation: $r = 0.89$; $n = 30$; P-value < 0.001). Therefore, we are confident that bird insectivore abundances represent a reliable measure for the feeding pressure on insect herbivores in our study and results are shown for the complete insectivorous bird community. However, despite the decrease in the abundance of insectivorous birds with increasing forest fragmentation we found no corresponding effect of forest fragmentation on insect herbivore abundances, neither for the bird exclosure nor for the control branches. This result conflicts with the findings of Karp *et al.* (2013) who showed that a decrease in the amount of natural forest area surrounding the coffee plantations and the simultaneous loss of insectivorous birds caused an increase in the number of coffee berry borers. Admittedly, insect herbivore abundances in our beating samples were notably low, which was supported by random visual inspections of the focal trees during the study period (F. Peter, personal observation). Nevertheless, low overall insect herbivore abundances may have circumvented the detection of differences between the treatments and along the degree of forest fragmentation. The low insect herbivore abundances may be explained by some not mutually exclusive factors, *e.g.* the comparably high rainfall from August to December 2012 (731 mm; 146 ± 38 mm/ mo) which may have reduced overall activity of herbivorous insects (Ezemvelo KZN Wildlife 2009). However, previous studies from the same region also found insect herbivore abundances to be rather low (Moran *et al.* 1994, Botzat *et al.* 2013, Peter *et al.* 2014) and possibly a result of seasonal variability within the insect herbivore community (da Silva *et al.* 2011). The picture of the insect herbivore community at the time of our sampling may thus not necessarily display the insect herbivore community throughout the whole season. Seasonal shifts in the insect herbivore community may have hampered a direct causal match of insect herbivore abundance and the degree in forest fragmentation and abundance of insectivorous birds, respectively. On the other hand, recent studies suggest that besides insectivorous birds, insectivorous bats may play an important role for the control of herbivorous insects as well (Kalka *et al.* 2008). Due to logistic constraints we were not able to open the bird exclosures at night or to install a higher number of bird exclosures to examine the effects of birds and bats separately. Thus, we are not able to exclude that insectivorous bats may have compensated for the loss of insectivorous birds in highly fragmented forests which in turn, may have blurred the effect of forest fragmentation on insect herbivore abundances (Kalka *et al.* 2008). However, there is still no consensus regarding the relative importance of insectivorous birds and bats for the trophic control of herbivorous insects (Kalka *et al.* 2008, Williams-Guillén *et al.* 2008, Karp *et al.* 2013). Similarly, recent studies suggest species-specific responses of insectivorous bats to increasing forest fragmentation. For example, Ethier & Fahrig (2011) found mixed responses of bats to the amount of forest and number of forest patches within the landscape. In contrast, a study of Estrada-Villegas *et al.* (2010) found changes in community composition and a decrease in feeding activity of insectivorous bats with increasing forest fragmentation. Thus, it remains rather speculative whether insectivorous bats may have compensated for the loss of insectivorous birds in highly fragmented forests and future studies further need to disentangle the trophic role of insectivorous birds and bats in fragmented forest landscapes. Finally, as we found an effect of forest fragmentation on LAL, we expect that in our study insectivorous bats did

not compensate for the loss of insectivorous birds. However, due to these not mutually exclusive reasons, the abundance of insect herbivores at a certain time may not be a representative measure to investigate effects of forest fragmentation and related changes in the abundance of insectivorous birds on lower trophic levels.

In contrast to the "snapshot" of insect herbivore activity covered by herbivore sampling, LAL comprises the accumulation of feeding events over a longer period (da Silva *et al.* 2011, Peter *et al.* 2014). In fact, in contrast to the lack of an effect of forest fragmentation and the treatment on the abundance of herbivorous insects, our results indicate higher LAL for the bird exclosure treatment and an increase in LAL on the control branches with increasing forest fragmentation. Overall, the effect of forest fragmentation on LAL is in line with the study of Karp *et al.* (2013) who found increased berry infestation rates with the loss of natural forest cover and implies an indirect effect of forest fragmentation on LAL through the loss of insectivorous birds. In the long-term, the fragmentation of forests may have consequences for the performance of plant individuals and forest tree communities as a result of increased levels of LAL.

Altogether, our results suggest that the fragmentation of indignous forests triggered cascading effects on tritrophic interactions between insectivorous birds, herbivorous insects and plants ultimately increasing levels of LAL. Hence, community patterns and interactions across multiple trophic levels in both subtropical indigenous forests and agroforestry systems seem to be comparably susceptible to fragmentation processes on the landscape scale. Therefore, conservation efforts should focus on the maintenance of continuous indigenous forests that are well-connected to smaller forest fragments on the landscape scale. Consequently, this will enhance the provisioning of food and nesting resources within forests, reduce edge effects and increase landscape connectivity which, in turn, will benefit species persistence and diversity and thus, complex trophic networks and associated ecosystem functionality.

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Chapter 4

Does herbivory cause a growth-defence trade-off in plants at different levels of nutrient availability?

with Franziska Peter, Dana G. Berens, Nina Farwig

a similar version of this manscript has been submitted to *Oecologia*

Summary

Plant defences against herbivory include compensatory growth as well as the production of defence compounds and have been suggested to depend on nutrient availability. However, it is unknown whether plants subject to herbivory favour either growth or defence and whether nutrient availability alters those patterns. To our knowledge, this is the first meta-analysis that synthesizes main and interactive effects of herbivory and nutrient availability on this *growth-defence trade-off* for grasses, herbs and woody species.

To do so, we performed mixed-effects meta-regressions and included differences in experimental study conditions as well as plant phylogenies. Our results showed that effects of herbivory and nutrient availability on plant growth and defence varied across plant types and differed with respect to the intensity of herbivory and study duration, respectively.

All plants subject to low-intensity herbivory fully compensated for the loss in aboveground biomass, whereas high-intensity herbivory significantly reduced aboveground biomass. Moreover, natural herbivory increased plant defences, whereas artificial herbivory failed to elicit the same response. Finally, high nutrient availability promoted a short-term increase in aboveground biomass for grasses and herbs and caused a short-term decrease in plant defences of herbs and woody species. Despite those main effects, we rarely found significant interactive effects of herbivory and nutrient availability, which indicates that nutrient availability does not seem to alter effects of herbivory.

Altogether, the findings of our meta-analysis imply that *growth-defence trade-offs* are less common as previously suggested and call for studies that tackle *trade-offs* on the physiological level, *e.g.* photosynthetic activity and chemical pathways.

Introduction

Herbivory is known to have profound effects on the performance of plants including photosynthetic activity, phytochemistry, metabolism, growth and reproduction (Karban & Myers 1989, Nykänen & Koricheva 2004, Boege & Marquis 2006). Consequently, herbivory may strongly affect the individual fitness, the persistence of plant species, biotic interactions as well as the structure and functioning of plant-based ecosystems (Coley *et al.* 1985, Marquis 2004, 2005).

Plants have evolved different mechanisms to defend themselves against herbivory. More specifically, plants are able to increase their photosynthetic activity and alter the acquisition and allocation of resources in response to herbivory (Nykänen & Koricheva 2004). In turn, this enables the compensation for lost biomass through increased growth rates (compensatory growth) and thus, to tolerate herbivory to a certain degree (Hawkes & Sullivan 2001). In addition to tolerance, plants show resistance against herbivores through induced production of secondary metabolites that act as defence compounds and deter herbivores from feeding on plants (Karban & Baldwin 1997, Nykänen & Koricheva 2004). Hence, tolerance through compensatory growth minimizes damages caused by herbivory in the past, while resistance through induced production of defence compounds simultaneously reduces the probability of future herbivory.

There is still no consensus on the effects of herbivory on plant growth and defence. For instance, the effect of herbivory has been suggested to range from increased plant mortality (*e.g.* Fine *et al.* 2006) to an "advantage of being eaten", *i.e.* promoted plant growth in response to herbivory (Belsky 1986, Paige & Whitham 1987, Järemo *et al.* 2007). This inconsistency may be due to the fact that plant responses to herbivory depend on the availability of resources, in particular on soil nutrient availability (Bryant *et al.* 1983, Coley *et al.* 1985, Chapin *et al.* 1990, Hawkes & Sullivan 2001). As soil nutrient availability is usually limited and characterized by a heterogeneous distribution, plants have been suggested to reallocate resources in favour of either compensatory growth or induced defence, commonly termed as *growth-defence trade-off* (Coley *et al.* 1985, van der Meijden *et al.* 1988, de Jong & van der Meijden 2000, Fine *et al.* 2006, Leimu & Koricheva 2006). In general, a *growth-defence trade-off* has been suggested to be more likely when either the degree in herbivory is high or when resources are limited (Valverde *et al.* 2003, Leimu & Koricheva 2006).

To our knowledge, there is only one comparative study which investigated the main and interactive effects of herbivory and nutrient availability on plants (*see* Hawkes and Sullivan 2001). In accordance with the above assumptions, findings of this meta-analysis showed that both the absence of herbivory and high nutrient availability increase overall plant growth (Hawkes & Sullivan 2001). However, while monocot herbs grow more after herbivory in high

resource conditions dicot herbs and woody species perform better in low resource conditions (Hawkes & Sullivan 2001). In general, the study showed that plant responses to herbivory and nutrient availability in terms of compensatory growth are complex and vary with respect to plant type. In contrast, knowledge on effects of herbivory on the induced production of plant defences is scarce. Moreover, it is vital to disentangle under which conditions plants subject to herbivory allocate resources in favour of either compensatory growth or induced defence. In particular, the relative significance of nutrient availability for resource allocation to growth and defence in undamaged plants and plants subject to herbivory is unknown. Thus, here we present a comprehensive meta-analysis that studies the main and interactive effects of herbivory and nutrient availability on growth and defence responses of plants in the light of a hypothesized *growth-defence trade-off*.

To further increase reliability of results and conclusions derived from this meta-analysis, we applied some methodological approaches, some of which are new in the field of ecological meta-analysis (Chamberlain *et al.* 2012, Zvereva & Kozlov 2014). Firstly, meta-analyses that combine different measures of plant growth (*e.g.* biomass, height, leaf area or number of branches; Hawkes and Sullivan 2001, Nykänen and Koricheva 2004, Massad 2013) or even measures of plant growth, photosynthesis and reproduction (Massad 2013) may blur specific responses of plants to herbivory and resource availability (Ferraro & Oesterheld 2002, Nykänen & Koricheva 2004). Therefore, we investigated effects on individual plant responses separately. Secondly, the time since the incident of herbivory and the nutrient treatment (*e.g.* Hawkes and Sullivan 2001, Ferraro and Oesterheld 2002, Massad 2013) as well as the intensity and the frequency of herbivory may strongly affect the specific outcome of plant responses (Ferraro & Oesterheld 2002). Thus, we explicitly incorporated these experimental study conditions, which has rarely been applied in meta-analyses yet (Zvereva & Kozlov 2014). Third, particularly defence mechanisms against herbivores have been suggested to be phylogenetically conserved and therefore similar for closely related plant species (Harvey & Purvis 1991, Silvertown & Dodd 1996). To control for species-specific effects as well as non-independence of effect sizes we applied a phylogenetic approach (Chamberlain *et al.* 2012).

The aim of our study was to investigate whether herbivory causes a *growth-defence trade-off* in grasses, herbs and woody species. If so, we were interested whether different levels of nutrient availability alter patterns of a potential g*rowth-defence trade-off*. To infer information on the underlying mechanism of nutrient acquisition and allocation in response to herbivory and nutrient availability, we additionally included effects on nitrogen concentration of plants. We performed mixed-effects meta-regressions and applied methodological approaches to reduce the heterogeneity across effect sizes and to infer reliable conclusions from the meta-analysis (see Hawkes and Sullivan 2001, Zvereva *et al.* 2010, Massad 2013). Altogether, the results of our meta-analysis will contribute to the knowledge on the phytocentric view on plant-herbivore interactions.

Methods

Literature survey & criteria for inclusion

To perform a comprehensive survey for publications that investigated the main and interactive effects of herbivory and nutrient availability on plant growth, plant defences and nitrogen concentration, we searched the web for publications using the ISI web of knowledge in September 2014. As studies usually measured plant defences and nitrogen concentration simultaneously we applied two separate searches, *i.e.* the first for plant growth and the second for plant defences and nitrogen concentration. For the first literature survey we used the following search string: ("simulated herbivory" OR (clipping AND herbivor*) OR defoliation) AND (fertili?ation OR fertili?er OR resource* OR nutrient* OR nitrogen) AND (growth OR biomass OR "dry weight" OR root*shoot OR RGR OR height OR length). The question mark covers different spelling types that use either "s" or "z" and the asterisk is a wildcard for the ending of the word. For the second literature survey we slightly adapted the first search string by substituting the third query by (secondary metabolite* OR tannin* OR alkal* OR phenol* OR terpen* OR flavon* OR carbon OR carotin* OR nitrogen). The two searches resulted in 1,686 and 1,592 publications, respectively. We reviewed all publications to select those that fulfilled the following criteria:

1. We only included studies that applied a fully crossed 2*2-factorial study design with at least two levels of herbivory and nutrient availability, respectively, resulting in four treatment combinations being (a) H0/N0 – control, *i.e.* no/low herbivory and no/low nutrient availability,

(b) H1/N0 – high herbivory and no/low nutrient availability, (c) H0/N1 – no/low herbivory, high nutrient availability, and (d) H1/N1 – high herbivory and high nutrient availability. Further, we omitted studies if the data required for the meta-analysis (mean, standard error/deviation, sample size) were not given in the publication and if we were not able to retrieve the data through personal communication.

2. We included studies that applied either artificial herbivory, natural herbivory or both. The advantage of artificial herbivory by manual removal of plant parts is the comparability of the effect of one herbivory level across the two levels of nutrient availability, *i.e.* the exact same degree of herbivory for H1/N0 and H1/N1 (Osier & Lindroth 2001, Erbilgin *et al.* 2014). Artificial herbivory and therefore, comparable levels of herbivory eliminate the possibility that differences in herbivory levels may confound effects of the two levels of nutrient availability (Wise & Abrahamson 2005). However, natural herbivory by insect herbivores has been suggested to elicit a different response in plants compared to mechanical damage through artificial herbivory (Felton & Tumlinson 2008, Pankoke & Müller 2013). Thus, we also included studies that applied natural herbivory (*e.g.* by grasshoppers, moths) in addition to artificial herbivory or as the sole herbivory treatment. However, we only included the latter studies if the degree of herbivory was reported and comparable for the two levels of nutrient availability (*e.g.* H1/N0 and H1/N1). This approach increased the sample size and enabled us to investigate the general role of elicitors of herbivores for plant responses. To account for potential differences between effects of artificial and/or natural herbivory we incorporated this factor as a moderator in the meta-analysis (see below).
3. We included studies that controlled the two levels of nutrient availability through the application of organic (*e.g.* dung, manure, refuse dumps of ants) or inorganic nitrogen sources (*e.g.* pellets, nutrient solutions). We did not consider studies that used a treatment with/without mycorrhizae as interactions between different types of mycorrhizae and vascular plants are complex and may change depending on herbivory and nutrient availability (Barto & Rillig 2010, Borowicz 2013). Further, we solely considered nutrient availability and did not combine nutrient availability with other resource types (*e.g.* water, light) as that may bias overall results (Halaj & Wise 2001, Wise & Abrahamson 2005). Analogue to the herbivory treatment, the type and the level of low and high nutrient availability were identical for the two treatment levels of herbivory (*e.g.* H0/N1 and H1/N1).
4. We only included studies that investigated effects on individual plant species instead of a vegetated patch without differentiation into species. The plant species of interest were terrestrial vascular plants with native origin (indigenous to the study location). We did not consider exotic/invasive plant species, water plants and algae or crops as the number of studies would not have sufficed for subgroup analyses. Moreover, including all plant species irrespective of any grouping may bias results as the plant responses to herbivory and nutrient availability may vary with those plant groups (*e.g.* algae vs. crops, Qing *et al.* 2012).

Altogether, 83 publications fulfilled the above criteria. Based on this set of studies, we established a data matrix containing factors describing the study and the experimental study conditions as well as the empirical data needed for the calculation of effect sizes. If a publication simultaneously included treatments with other abiotic or biotic factors (*e.g.* light/water availability) we only considered the effects of herbivory and nutrient availability in the optimum level(s) of the other treatment factor(s) (*e.g.* optimal availability of light and water). Moreover, if the study design included more than two treatment levels of herbivory or nutrient availability we chose the lowest and the highest level. Subsequently, we focused on the most frequent measures for plant growth, plant defence and nitrogen concentration to increase the predictive power and thus, the reliability of results derived from the meta-analysis. In terms of plant growth, biomass (above-/below-ground, total) and the root:shoot ratio were the most frequent responses. However, total biomass and the root:shoot ratio combine above- and below-ground responses and may thus, blur specific plant responses. Hence, we only included studies that measured above- and below-ground biomass as individual plant responses. For the defence response, we included studies that measured the concentration of secondary metabolites (defence compounds) in aboveground plant parts. Here, the most frequent measures for plant defences were tannins, glycosides and total phenolics. Finally, we included studies that measured nitrogen concentration in aboveground plant parts and excluded publications that measured nitrogen concentration in below-ground plant parts or

at the whole-plant level. The individual measures of plant responses are hereafter referred to as response categories.

The above restrictions condensed the data set to 61 publications (Appendix 4.1). Some publications provided two or more independent study cases, *e.g.* owing to different plant species, origin of plant populations, study locations. However, we only split publications into more than one study case if the study design provided all four independent treatment combinations for each study case. Thus, the 61 publications provided 124 study cases, while subsets provided data for individual meta-regressions on the respective response categories (Appendix 4.2): 78 study cases for aboveground biomass, 62 study cases for below-ground biomass, 30 study cases for defence compounds and 46 study cases for nitrogen concentration in aboveground plant parts. With respect to the growth response and nitrogen concentration, the number of study cases equals the sample size (k) for the respective meta-regression models. However, the majority of studies that investigated effects on plant defences measured more than one defence compound (*e.g.* tannins, glycosides) per study case and thus, the same set of plant individuals. Despite the nestedness of data, we decided to include the concentration of more than one defence compound per study case for two reasons. First, a recent meta-analysis suggested that resource allocation for individual secondary metabolites and their simultaneous production is not constrained by *trade-offs* (Koricheva *et al.* 2004). Second, effects of herbivory and nutrient availability on the concentration of individual secondary metabolites may vary as a result of differences in their chemical structure (*e.g.* nitrogen-/carbon-based) and their chemical pathway (Keinanen *et al.* 1999, Konno 2011). Owing to the suggested independence of individual secondary metabolites, we aimed to ascertain the mean overall response in plant defence, which yielded a sample size of $k = 59$ (tannins: $k = 27$, glycosides: $k = 21$, total phenolics: $k = 11$). However, to account for the nested structure of defence compounds per study case we implemented an additional random factor (see method section).

Data acquisition & calculation of effect sizes

To calculate the individual effect sizes for the main and the interactive effects of herbivory and nutrient availability for every response category per study case we gathered the mean and the standard deviation (*sd*) as well as the sample size for every treatment combination. Mean values and *sd* (or standard error) were either taken from tables and figures (using Web Based Plot Digitizer version 3.7) given in the publications or retrieved through personal communication. The effect size was calculated as *Hedges' d* (Gurevitch *et al.* 2000, Hawkes & Sullivan 2001, Morris *et al.* 2007). We chose *d* as it is a common standardized effect size and incorporates both the sampling variances for each treatment combination and a correction factor for small sample sizes within studies. Moreover, the standardized effect size *d* allows a comparison of effect sizes across studies that use dependent variables measured on different scales (Breaugh 2003). We calculated one effect size for the main effect of herbivory (d_H) and nutrient availability (d_N) as well as one effect size for their interactive effect (d_{HN}), *i.e.* three effect sizes per response category per study case.

Based on the definition of Morris *et al.* (2007), the effect size of one treatment factor (*e.g.* herbivory) is the difference between the mean of the response category for the two levels of the treatment factor, *e.g.* H0 and H1. Due to the full factorial study design, we included the means (M) of all four treatment combinations, being M_C (H0/N0), M_H (H1/N0), M_N (H0/N1), M_{HN} (H1/N1). The expression for the mean difference for the calculation of the effect sizes d_H and d_N is based on Morris *et al.* (2007) who applied a slight modification to effect size measures of Gurevitch *et al.* (2000). In our meta-analysis, a positive value for d_H and d_N indicates a positive response to herbivory and nutrient availability, respectively and *vice versa* (Appendix 4.3). Similarly, we adjusted the expression for the mean difference for d_{HN} in a way that a positive effect size indicates that herbivory has a greater effect at high nutrient availability and *vice versa* (Appendix 4.3).

Statistical analyses

We performed mixed-effects meta-regressions to investigate the main and interactive effects of herbivory and nutrient availability on the *growth-defence trade-off* in plants. The choice of mixed-effects meta-regressions enabled us to incorporate both random and fixed effects (moderators). We fitted the meta-regression models with restricted maximum likelihood and the Knapp and Hartung adjustment where individual coefficients and confidence intervals are based on a *t*-distribution with $k - p$ degrees of freedom, with k and p being the sample size and the number of coefficients included in the model, respectively (Knapp & Hartung 2003, Viechtbauer 2010). We

fitted three meta-regression models for the main and interactive effects of herbivory and nutrient availability for each response category, *i.e.* separate models for d_H, d_N and d_{HN} for (1) aboveground biomass, (2) below-ground biomass and (3) the concentration of defence compounds and (4) the nitrogen concentration in aboveground plant parts. Besides the effect size, we defined the sampling variance *s'* and weights (inverse of the sampling variance *s'*) for the meta-regression models (Gurevitch *et al.* 2000; Appendix 4.3).

To account for specific differences in experimental study conditions relevant to the applied treatments of herbivory and nutrient availability we incorporated fixed factors (moderators). We included 'plant type' and 'study duration' as moderators for all meta-regression models. We defined 'plant type' based on the assignment of plant species to one of the three mutually exclusive plant types, *i.e.* grasses, herbs, and woody species (including shrubs and trees) using online information of the United States Department of Agriculture (http://plants.usda.gov/java/factSheet). Overall, the 62 publications included 76 different plant species (Appendix 4.2), which were categorized as grasses (33 species), herbs (21 species) or woody species (22 species). We did not apply further discrimination of herbs into monocot and dicot herbs and of woody species into shrubs and trees, respectively, as the individual sample sizes for monocot herbs and shrubs would not have sufficed for subgroup analyses (Appendix 4.2). Across the response categories, the sample size for grasses, herbs and woody species were comparable (Appendix 4.2). Unfortunately, there were no studies that investigated effects of herbivory and nutrient availability on defence compounds of grasses. Similarly, only one study investigated effects of herbivory and nutrient availability on defence compounds in herbs. We further defined 'study duration' as the time between the last incident of herbivory or nutrient addition and the measurement of the respective plant response. We specified short-term responses as responses after one to ten weeks and long-term responses as responses after more than ten weeks up to one year. In addition to 'plant type' and 'study duration', we included 'intensity of herbivory' and 'frequency of herbivory' as moderators for meta-regression models on d_H and d_{HN}. To combine the different approaches of applied herbivory (*e.g.* single/multiple events of clipping leaves/mowing), we generated new indices differentiating between low-/high-intensity herbivory and infrequent/frequent herbivory. We specified low-intensity herbivory as the removal of 10% to 50% plant biomass and mowing to a height of 5 cm to 10 cm aboveground. Accordingly, we specified high-intensity of herbivory as the removal of more than 50% plant biomass and mowing to less than 5 cm aboveground. Similarly, we specified single and multiple herbivory events as infrequent and frequent herbivory, respectively. Finally, with respect to the defence response we included the 'type of herbivory' (artificial, natural, both) as a moderator for meta-regression models on d_H and d_{HN}. Based on Pearson's correlation there was no collinearity among the moderators.

To choose the moderator(s) that yielded the best model fit for every meta-regression model, we applied automated model selection. The automated model selection finds the best models (confidence set of models) among all possible models (candidate set of models) through exhaustive screening (Calcagno & de Mazancourt 2010). The models are fitted with the specified fitting function, here mixed-effects meta-regression, and ranked by the specified Information Criterion, here the Akaike Information Criterion for small sample sizes (AICc, Cavanaugh 1997) and corresponding weights. We set a constraint on the candidate set of models, which was not to include more than two moderators per meta-regression model. We applied this restriction as the specification of one moderator often contained both specifications of another moderator, *e.g.* changes in biomass of grasses subject to either low- or high-intensity herbivory were measured after either short- or long-term responses. Thus, including more than two moderators per meta-regression model would have reduced sample size per subgroup and thus, explanatory power as well as overall information gain. Moreover, restricting the maximum number of moderators enabled us to identify the most important factors that moderate the individual plant responses.

As random factors we defined 'study' to account for the nested design of more than one study case (*e.g.* different plant species) per publication and thus, for heterogeneity across studies and homogeneity among study cases derived from the same study. As additional random factors we defined 'species' and 'phylogeny'. The specified random factors enabled us to explore how much variability across the individual effect sizes per study case is accounted for by the origin of data (*e.g.* study design, location of study), species taxonomic identity and phylogenetic relatedness across plant species. The random factor 'phylogeny' was based on phylogenetic distances including all plant species from the

respective data set for each response category. The phylogenetic distances were derived from a comprehensive phylogenetic tree we compiled for this study. To construct this tree, we used all plant species from our meta-analyses (Appendix 4.2) and a list of plant species from the comprehensive trait database GLOPNET (Wright *et al.* 2004), which contains 2,051 plant species. We chose this approach as comprehensive trees provide more reliable node ages and thus, phylogenetic distances between species than trees based on the set of study plant species alone (own observation). We constructed the tree using the online program Phylomatic version 3 (http://phylodiversity.net/phylomatic; Webb and Donoghue 2005) and the internal 'megatree' R20120829. Subsequently, we adjusted the branch lengths of our tree with the program Phylocom version 4.1 (Webb *et al.* 2008). In more detail, we used Phylocom to assign node ages to our phylogenetic tree based on the internal ages file 'Wikstrom ages', which contains node ages of angiosperms (Wikström *et al.* 2001). Based on our phylogenetic tree with adjusted branch lengths, we created one phylogentic distance matrix for each response category. To do so, we dropped all tips (plant species) from our tree that were not included in the data set of the respective meta-regression models. Based on those phylogenetic distance matrices we calculated correlation matrices, which we then incorporated in the respective meta-regression model as the random factor 'phylogeny'. Finally, for the meta-regression models on the concentration of defence compounds we included 'study case' as the fourth random factor to account for the nested structure of different defence compounds per study case.

The effect size d was considered significant when the 95% confidence intervals around the weighted means of *d* for the individual groups (*e.g.* grasses, herbs and woody species) did not overlap zero. Similarly, effect sizes for individual groups were significantly different from each other when their 95% confidence intervals around the weighted means of *d* did not overlap.

To assess the quality of the meta-regression models, we evaluated the results of the omnibus test of moderators (Q_M and the *P*-value $Q_M p$), where a $Q_M p$ smaller than 0.05 allows to reject the null-hypothesis that the mean effect sizes of the subgroups equal zero. Due to the Knapp and Hartung adjustment the omnibus test statistic uses an F-distribution with m and $k - p$ degrees of freedom, with m, k and p being the number of coefficients included in the omnibus test, the number of studies (sample size) and the number of coefficients included in the model, respectively (Viechtbauer 2010). Moreover, we used profile plots of the restricted log-likelihood to assess the performance of each random factor in the meta-regression models. Finally, we used funnel plot diagnostics and Rosenthal's fail-safe number (Rosenthal 1979) with alpha = 0.05 to evaluate the impact of publication bias. After Rosenthal (1991), a fail-safe number larger than $5 * k + 10$, with k being the sample size, is considered robust against publication bias. All statistical analyses were done using R version 3.2.0 (R Core Team 2015) with packages 'taxize' (Chamberlain & Szocs 2013), 'ape' (version 3.3, Paradis *et al.* 2004), 'metafor' (Viechtbauer 2010) and 'glmulti' (Calcagno 2013).

Results

Effects of herbivory on plant growth & defence

The effects of herbivory on above- and below-ground biomass were moderated by plant type in combination with intensity of herbivory (Tab. 1, Fig. 1): The aboveground biomass of all plants subject to low-intensity herbivory did not differ significantly from the aboveground biomass of control plants. In contrast, high-intensity herbivory significantly reduced the aboveground biomass of all plants. Furthermore, herbivory significantly reduced below-ground biomass of grasses for both levels of intensity. In contrast, the below-ground biomass of herbs and woody species did not differ significantly from control plants irrespective of intensity of herbivory. The effect of herbivory on plant defence was moderated by the type of herbivory in combination with intensity of herbivory (Tab. 1, Fig. 1): Natural herbivory at low intensity significantly increased the concentration of defence compounds, whereas artificial herbivory and the combination of natural and artificial herbivory did not affect the concentration of defence compounds.

Effects of nutrient availability on plant growth & defence

Throughout, effects of nutrient availability were moderated by plant type and study duration (Tab. 1, Fig. 1): While high nutrient availability caused a significant short-term increase in the above- and below-ground biomass of herbs and grasses, this was not the case for long-term studies. In contrast, nutrient availability did not affect above- and below-ground biomass of woody species irrespective of study duration. High nutrient availability significantly decreased the concentration of defence com-

Table 1: Results of the meta-regression models for the main and interactive effects herbivory and nutrient availability on plant growth, plant defence and nitrogen concentration.

Final meta-regression models for main and interactive effects of herbivory and nutrient availability on aboveground biomass (sample size: $k = 78$), below-ground biomass ($k = 62$), the concentration of defence compounds ($k = 59$) and nitrogen concentration ($k = 46$); plant type = grasses, herbs, woody species; H = herbivory; Q_M and $Q_M p$ refer to the output of the omnibus test of moderators, bold *P*-values indicate significant *P*-values ($Q_M p < 0.05$); Pb = publication bias based on Rosenthal's fail-safe number.

	Response category	Moderators	Q_M	$Q_M p$	Heterogeneity explained [%] by				Pb
					study	species	phylogeny	study case	
(1)	*d*(Herbivory)								
	Aboveground biomass	~ plant type + H intensity	4.4	**0.003**	79.3	< 0.0	20.7	nA	no
	Below-ground biomass	~ plant type + H intensity	7.1	**< 0.001**	100.0	< 0.0	< 0.0	nA	no
	Defence compounds	~ H type + H intensity	2.7	**0.042**	100.0	< 0.0	< 0.0	< 0.0	yes
	Nitrogen concentration	~ plant type + H frequency	3.9	**0.009**	100.0	< 0.0	< 0.0	nA	yes
(2)	*d*(Nutrient availability)								
	Aboveground biomass	~ plant type + study duration	2.7	**0.038**	90.4	< 0.0	9.6	nA	no
	Below-ground biomass	~ plant type + study duration	2.4	0.064	82.0	18.0	< 0.0	nA	no
	Defence compounds	~ plant type + study duration	12.3	**< 0.001**	< 0.0	100.0	< 0.0	< 0.0	no
	Nitrogen concentration	~ plant type + study duration	22.0	**< 0.001**	68.0	32.0	< 0.0	nA	no
(3)	*d*(Herbivory * nutrient availability)								
	Aboveground biomass	~ plant type + H intensity	1.2	0.308	17.3	< 0.0	82.7	nA	no
	Below-ground biomass	~ plant type + H frequency	0.5	0.706	< 0.0	< 0.0	100.0	nA	yes
	Defence compounds	~ plant type	5.3	**0.008**	< 0.0	< 0.0	100.0	< 0.0	yes
	Nitrogen concentration	~ plant type + study duration	1.4	0.261	59.7	1.7	38.6	nA	no

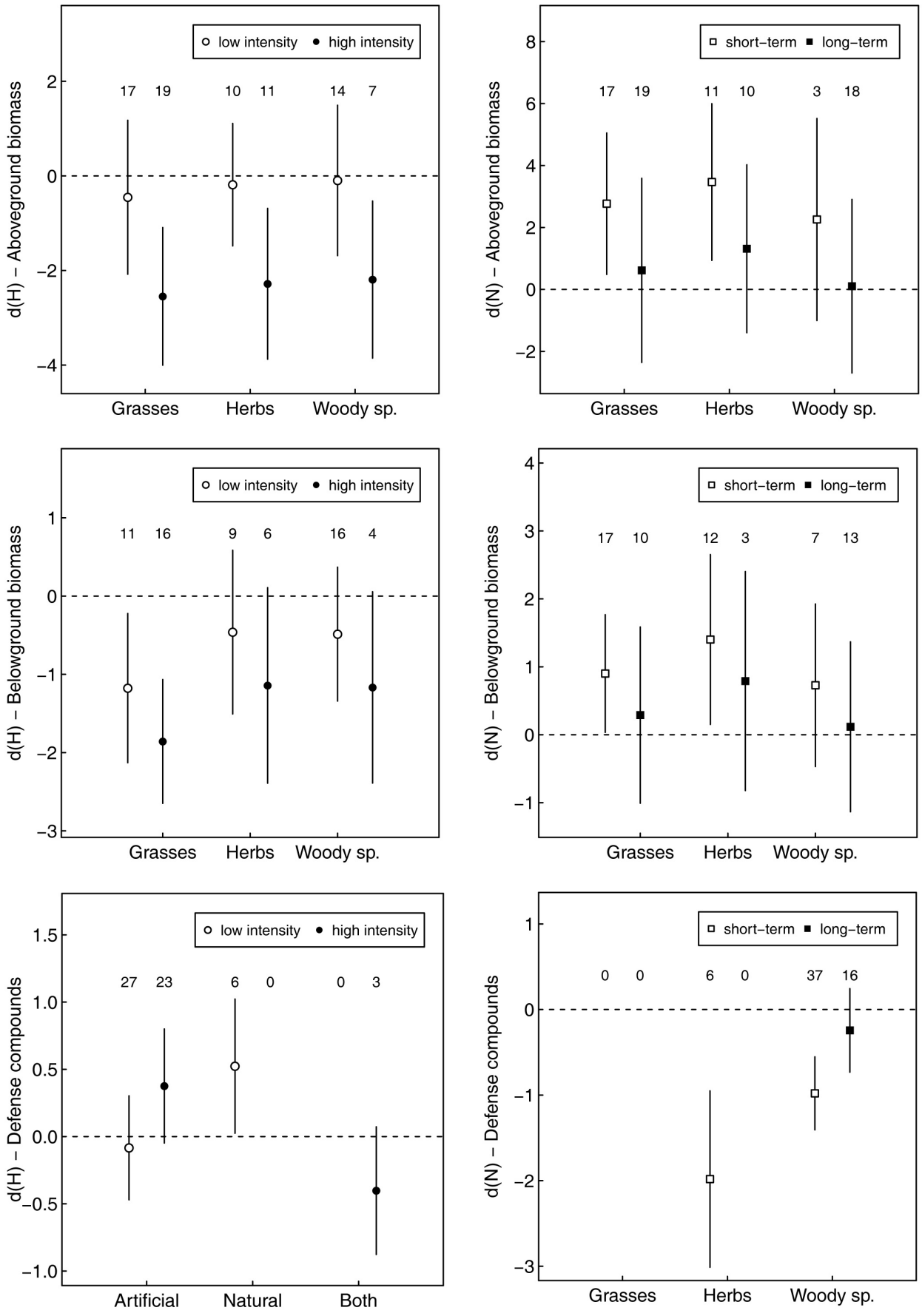


Figure description on next page.

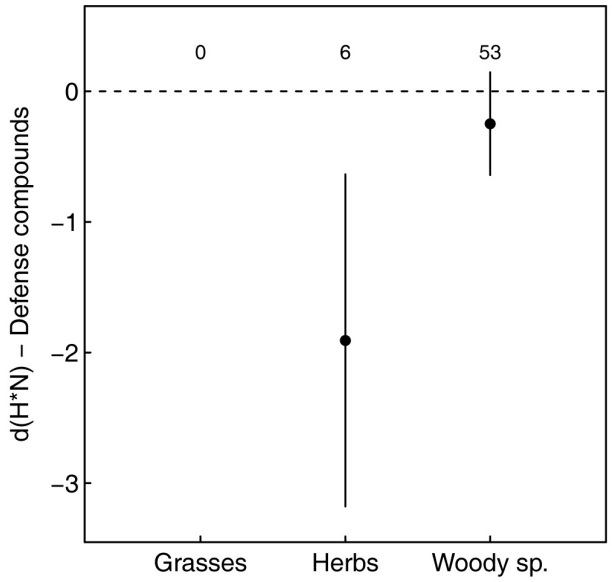
pounds of herbs and woody species at short study durations, whereas this was not the case for woody species at long study durations.

Interactive effects of herbivory & nutrient availability on plant growth & defence

There were no interactive effects of herbivory and nutrient availability on above- and below-ground biomass of plants (Tab. 1). However, herbivory and nutrient availability had a significant interactive effect on the concentration of defence compounds of herbs (Tab. 1, Fig. 2): The effect of herbivory on the concentration of defence compounds of herbs was smaller when nutrient availability was high. In contrast, there was no significant interactive effect of herbivory and nutrient availability on the concentration of defence compounds in woody species (Tab. 1, Fig. 2).

◄ Figure 1: *Hedges' d* for main effects of herbivory and nutrient availability on plant growth, and plant defence.

Effects of herbivory (left) differed across plant types or type of herbivory and depended on the intensity of herbivory; effects of nutrient availability (right) differed across plant types and depended on study duration; circles and squares depict weighted means of *Hedges' d*; bars represent the 95% confidence intervals around weighted *Hedges' d* per group; numbers indicate sample size per group.

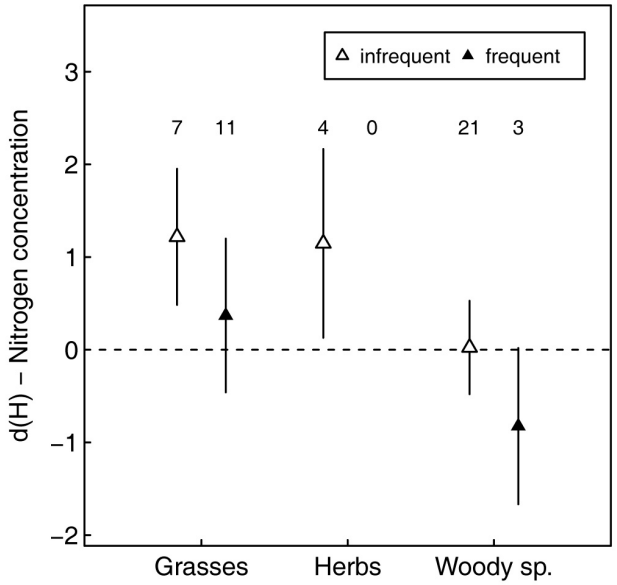


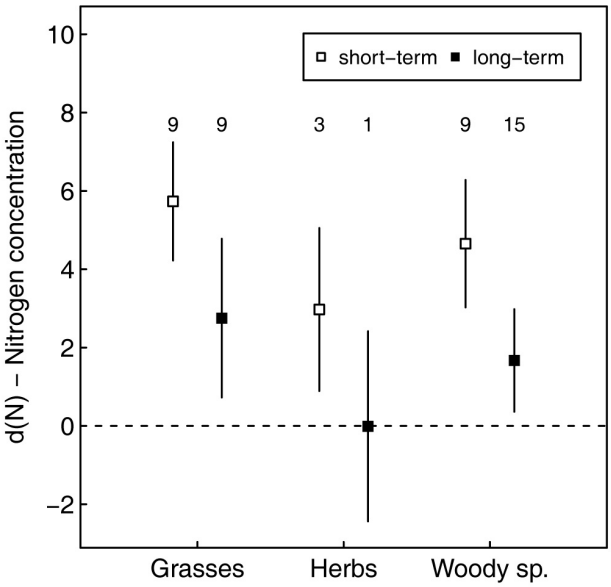
◄ Figure 2: *Hedges' d* for the interactive effect of herbivory and nutrient availability on plant defence.

Effects depended on plant type; circles depict weighted means of *Hedges' d*; bars represent the 95% confidence intervals around weighted *Hedges' d* per group; numbers indicate sample size per group.

▼ Figure 3: *Hedges' d* for main effects of herbivory and nutrient availability on the concentration of nitrogen.

Effects of herbivory (left) differed across plant types an depended on the frequency of herbivory; effects of nutrient availability (right) differed across plant types and depended on study duration; triangles and squares depict weighted means of *Hedges' d*; bars represent the 95% confidence intervals around weighted *Hedges' d* per group; numbers indicate sample size per group.





Effects of herbivory & nutrient availability on nitrogen concentration

The effect of herbivory on nitrogen concentration in aboveground plant parts was moderated by plant type in combination with frequency of herbivory (Tab. 1, Fig. 3): Infrequent herbivory significantly increased nitrogen concentration of grasses and herbs, whereas frequent herbivory did not affect nitrogen concentration of grasses. Further, nitrogen concentration of woody species subject to herbivory did not differ significantly from control plants irrespective of frequency of herbivory. The effect of nutrient availability on nitrogen concentration was moderated by plant type and study duration (Tab. 1, Fig. 3): High nutrient availability increased nitrogen concentrations of grasses and woody species independent of study duration. With respect to herbs, high nutrient availability only caused a short-term increase in nitrogen concentration. There was no interactive effect of herbivory and nutrient availability on nitrogen concentration (Tab. 1).

Discussion

Overall, herbivory and nutrient availability exerted strong effects on the performance of grasses, herbs and woody species. Across all plant types, low-intensity herbivory had no effect, whereas high-intensity herbivory significantly decreased aboveground biomass. Further, aboveground herbivory additionally caused a decrease in below-ground biomass of grasses at both intensity levels. Moreover, natural herbivory at low intensity increased the concentration of defence compounds of herbs, whereas artificial herbivory failed to elicit the same response. In contrast to herbivory, responses to nutrient availability depended on study duration: High nutrient availability promoted a short-term increase in above- and below-ground biomass of grasses and herbs and caused a short-term decrease in plant defences of herbs and woody species. Despite significant main effects we solely found one interactive effect of herbivory and nutrient availability with high nutrient availability causing a decrease in plant defences of herbs subject to herbivory.

Effects of herbivory on plant growth & defence

Effects of herbivory on aboveground biomass did not vary with respect to plant type but depended on the intensity of herbivory. More specifically, grasses, herbs and woody species subject to low-intensity herbivory were able to fully compensate for the loss of aboveground biomass. In contrast, high-intensity herbivory significantly decreased aboveground biomass of all plant types. This implies that the overall ability of plants for compensatory growth is limited and decreases with increasing degree of herbivory. At the same time, our results indicate that the ability of compensatory growth may be linked to nitrogen concentrations. Nitrogen concentrations of grasses and herbs increased due to alleviated herbivory, probably as a result of shifts in resource acquisition and allocation as well as increased photosynthetic activity (Nykänen & Koricheva 2004, Lestienne *et al.* 2006). Increased nitrogen concentrations have in turn, been suggested to promote nitrogen-demanding processes such as growth and thus, benefit full compensation of lost biomass (Nykänen & Koricheva 2004). In contrast, severe herbivory may cause a depletion of nitrogen sources available for reallocation, prevent an increase in nitrogen concentrations and thus, reduce the chances of full compensatory growth (Strengbom *et al.* 2003).

In contrast to aboveground biomass, effects of herbivory on below-ground biomass differed across plant types but not with respect to intensity of herbivory. Solely grasses showed a significant decrease in below-ground biomass in response to herbivory. This finding supports the assumption that above- and below-ground responses of plants should be considered separately (as opposed to common measures like the root:shoot ratio) to avoid biased conclusions. Furthermore, our findings indicate that consequences of aboveground herbivory on resource dynamics and therefore, growth patterns of grasses extend to the whole-plant level. In more detail, grasses seem to allocate resources favouring above- over below-ground growth when they experience herbivory (Bryant *et al.* 1983), which presumably is the most economic and efficient way to recover from herbivory. The close connection between spatially separated above- and below-ground compartments supports findings of reviews and meta-analyses, that suggest tight links and complex trophic interactions between spatially separated biota, *i.e.* between insect herbivores and soil decomposers linked *via* plants (*e.g.* A'Bear *et al.* 2014, Johnson *et al.* 2012).

The concentration of defence compounds was significantly affected by natural herbivory but not by artificial herbivory or the combination of natural and artificial herbivory. Thus, our finding supports the hypothesis that artificial herbivory may not necessarily elicit the same plant responses as natural herbivory. Induced defences may strongly

depend on certain cues such as chemical compounds specific to the saliva of herbivores (Karban & Baldwin 1997, Felton & Tumlinson 2008, Pankoke & Müller 2013). Interestingly, the combination of artificial and natural herbivory did not affect the concentration of defence compounds either. However, in the respective studies the proportion of natural herbivory due to actual herbivores was low compared to the simultaneous application of artificial herbivory (*e.g.* Lindroth *et al.* 2007, Hódar *et al.* 2008, Stevens *et al.* 2014). Therefore, cues of natural herbivory may not have sufficed to elicit the same defence response as the sole application of natural herbivory. As the production of defence compounds is costly to the plant, economic and efficient resource allocation is vital and therefore, the production of defences should only be induced in response to herbivory (Karban & Baldwin 1997).

Altogether, plants subject to low-intensity herbivory fully compensated for the loss in aboveground biomass and partially showed induced defence with respect to natural herbivory. Hence, at least with respect to low-intensity herbivory, plant responses may not necessarily indicate a *growth-defence trade-off*.

Effects of nutrient availability on plant growth & defence

Effects of nutrient availability on plant growth varied for grasses, herbs and woody species and changed over time. Shortly after the resource pulse, high nutrient availability resulted in increased above- and below-ground biomass of grasses and herbs. Accordingly, high nutrient availability may benefit short-term growth rates of grasses and herbs and thus, biomass accumulation. However, ongoing exploitation of nutrients in the course of time may lead to a depletion of soil nutrients. Thus, resource pulses may be short-lived and effects of high nutrient availability may diminish in the long-term (Frost & Hunter 2008). In turn, this may cause similar long-term growth rates across nutrient treatments accompanied by aligned above- and below-ground biomass. This is supported by the finding that the short-term effect of nutrient availability on the nitrogen concentration of grasses, herbs and woody species tended to be more pronounced as well. The lack of an effect of nutrient availability on the growth of woody species may be due to the inherently slow growth rates of woody species compared to grasses and herbs (Hunt & Cornelissen 1997). Therefore, woody species may well benefit from high nutrient availability, as indicated by the short-term increase in nitrogen concentration, but significant differences in above- and below-ground biomass may only become apparent over longer time scales than applied in the studies (Leimu & Koricheva 2006).

Similarly to plant growth, the defence response of herbs and woody species was affected by nutrient availability and changed over time. In more detail, high nutrient availability caused a short-term decrease in the concentration of defence compounds of herbs and woody species. Overall, there is an ongoing debate on different coexisting hypotheses proposed to explain patterns in plant defences (Berenbaum 1995, Hamilton *et al.* 2001, Endara & Coley 2011). Particularly the more pronounced short-term effects of nutrient availability on plant growth and defence are in line with the *resource availability hypothesis* (RAH, Coley *et al.* 1985). The RAH predicts that the optimal level of defence investment increases as the realized growth rate of the plant decreases (and *vice versa*). Considering short-term responses of herbs, high nutrient availability promoted above- and below-ground growth and decreased the production of plant defences.

Altogether, in response to high nutrient availability and increased nitrogen concentration, respectively, particularly herbs seem to further optimize their growth at the expense of defence. Hence, with respect to the effect of nutrient availability on plant performance our results partially support the existence of an apparent *growth-defence trade-off*. Yet, against general expectations high nutrient availability rather amplified the *growth-defence trade-off*.

Interactive effects of herbivory & nutrient availability on plant growth & defence

In contrast to the significant main effects, we rarely found significant interactive effects of herbivory and nutrient availability on plant performance. First, nutrient availability did not alter effects of herbivory on aboveground biomass and thus, compensatory growth. Neither did nutrient availability affect below-ground growth and thus, mitigate the decrease in below-ground biomass of grasses subject to herbivory. This is supported by the lack of an interactive effect on nitrogen concentration of plants. Altogether, the above findings are in line with the meta-analysis of Hawkes and Sullivan (2001), who found that herbivory and nutrient availability had no interactive effect on plant growth. However, in contrast to plant growth, herbivory and nutrient availability had a significant interactive effect on the defence response of herbs.

In more detail, the effect of herbivory on the concentration of defence compounds of herbs was smaller when nutrient availability was high. Thus, high nutrient availability may drive fast-growing species such as herbs to further optimize their compensatory growth in response to herbivory rather than to invest in the production of defences. Again, this is in line with the RAH which suggests fast-growing species to reach their maximum growth at low levels of defence (Coley *et al.* 1985). However, the concentration of defence compounds of woody species subject to herbivory did not change in response to nutrient availability. This supports the hypothesis that slow-growing species such as woody species rely on the production of defence compounds and thus, do not shift to promoted growth at the expense of defence at high nutrient availability. Hence, our results partially support the existence of a *growth-defence trade-off* but suggest that it may not be as common as previously suggested (Leimu & Koricheva 2006).

Conclusions

Our meta-analysis corroborates the assumption that herbivory and nutrient availability exert strong effects on the performance of grasses, herbs and woody species, ranging from shifts in resource allocation to ultimate consequences for plant growth and defence. Moreover, our findings show that the magnitude of the effects of herbivory and nutrient availability on plant performance is strongly driven by specific conditions such as the intensity of herbivory and the time frame under consideration. This shows that future meta-analyses should explicitly address moderators relevant to the measured effect size. Our findings may further contribute to management implications for grassland ecosystems. For instance, low-intensity herbivory (or defoliation) allows plants to fully recover from the loss in aboveground biomass but at the same time, maintains plant diversity, *i.e.* by particularly affecting growth patterns of grasses at the whole-plant level. Further, nitrogen fertilization promotes short-term growth rates and thus, may benefit grassland productivity. However, higher nutrient availability does not affect the performance of plants that experience herbivory, which implies that fertilization or increased nitrogen deposition in grassland and forest ecosystems may not necessarily alleviate the impact of herbivory.

Despite the significance of herbivory and nutrient availability for plant performance, different levels of nutrient availability rarely modified effects of herbivory. Moreover, findings of our meta-analysis only partially support the hypothesized *trade-off* between growth and defence in plants. Recently, Massad *et al.* (2012) suggested that *trade-offs* more likely take place at the physiological level, including photosynthetic activity and chemical pathways, in contrast to growth rates and concentrations of defence compounds. Accordingly, this may explain why *trade-off* patterns were less pronounced in our meta-analysis. Future studies should attempt to unravel underlying mechanisms of effects of herbivory and nutrient availability on physiochemical, physiological and morphological plant responses at the whole-plant level. Moreover, ecological approaches are needed to ascertain whether changes in plant performance due to herbivory and nutrient availability cause long-term shifts in plant-based ecosystems or create feedback effects on herbivore communities.

Acknowledgement

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CHAPTER 5

Synthesis

For centuries, humans extensively used and profoundly altered ecosystems at a global scale, which is assumed to have serious implications for ecosystem functioning and human-well being. Amongst others, it has been suggested that deforestation and the associated process of forest fragmentation have severe and multi-faceted consequences entailing an overall loss in biodiversity, the disruption of trophic interactions and impaired functioning of forest ecosystems. Eventually, consequences of forest fragmentation may threaten ecosystem stability and ecosystem services of forests.

Insect herbivores are known to play a key role in all plant-based ecosystems, *i.e.* they affect growth, fitness and reproduction of plant individuals and thus, have been suggested to influence plant species persistence as well as the structure and composition of plant communities. Hence, changes in insect herbivore communities due to forest fragmentation, particularly increased insect herbivore abundances, may cause an overall increase in the susceptibility of plants to insect herbivory with severe consequences for forest ecosystems. So far, there is no consensus regarding the implications of forest fragmentation for plant-herbivore interactions. Findings of previous studies indicate inconsistent responses of insect herbivores to forest fragmentaion and the ultimate degree of insect herbivory in fragmented forest landscapes varies correspondingly.

With this thesis, I aimed to unravel the discrepancy in the above findings by addressing the context-dependency and the complex nature of antagonistic plant-herbivore interactions, which may both cause spatial variability. To address the context-dependency of plant-herbivore interactions, I conducted two field studies in a subtropical forest landscape in southern KwaZulu-Natal (South Africa). The first field study aimed at disentangling potential interactive effects of forest fragmentation on the landscape scale and local tree diversity on plant-herbivore interactions and the associated process of insect herbivory. With the second field study, I examined the trophic control of herbivorous insects through insectivorous birds along a gradient of increasing forest fragmentation including ultimate consequences for the degree of insect herbivory. Finally, to address the complexity of plant-herbivore interactions, I performed a comprehensive meta-analysis on plant responses to insect herbivory and thus, feedback effects on insect herbivores as well as the potential of plants to mediate the outcome of plant-herbivore interactions.

Interactive effects of forest fragmentation & tree diversity

Recently, studies suggested that co-occurring environmental drivers may not only affect species communities and trophic interactions simultaneously, but also in an interactive manner creating synergistic or antagonistic effects. In addition to forest fragmentation, the quantitative and qualitative availability of host-trees (*i.e.* tree diversity) plays an important role for insect herbivore communities. So far, previous studies ascertained conflicting effects of both forest fragmentation and tree diversity on plant-herbivore interactions, which may be owed to complex interactive effects, albeit both drivers act on different spatial scales. Across ten forest patches that covered a gradient of increasing forest fragmentation, I monitored the tree diversity per forest patch. Subsequently, I collected standardized beating samples across an array of different tree species to derive information on the community composition, species richness and abundance of insect herbivores per tree species. Finally, I assessed the degree of herbivory for the respective tree species. Species richness decreased while the abundance of insect herbivores increased with increasing tree diversity in slightly fragmented forests. This finding implies that insect herbivores benefit from dispersing across the variety of host-tree species, which in turn, reduces species richness per host-tree species accompanied by increased species abundances. Interestingly, the effect of tree diversity diminished with increasing forest fragmentation, presumably due to changes in the community composition of insect herbivores with increasing forest fragmentation. Within the family of Curculionidae, smaller species were gradually substituted by larger species with increasing forest fragmentation, which implies *environmental filtering* based on dispersal ability. Smaller insect herbivores show lower dispersal ability associated with reduced migration and recolonization events between forest isolates and therefore, may be more susceptible to forest fragmentation. In contrast, larger species may be able to traverse an inhospitable landscape matrix between forest isolates and further, may be less sensitive to differences in host-tree availability at small spatial scales. Despite the effects on insect herbivore communities, there was no effect on the ultimate degree of insect herbivory which may be explained by non-mutually exclusive factors, *e.g.* seasonal shifts in insect herbivore populations and their feeding habits. Nevertheless, findings of this field study revealed a striking pattern with respect

to interactive effects of co-occurring environmental drivers that act on different spatial scales: Changes in tree diversity determined the direction of the effect whilst the degree of forest fragmentation determined the magnitude of the effect on insect herbivore communities.

Ecological function of predators in fragmented forests

Insectivorous birds play a crucial role for the trophic control of insect herbivores and thus, for the ultimate degree of insect herbivory in forest ecosystems. However, increasing forest fragmentation threatens the ecological function of insectivorous birds and has been suggested to cause cascading effects across multiple trophic levels, *e.g.* insect herbivores and plants. To unravel the above coherences, I selected 15 forest patches that covered an increasing gradient of forest fragmentation and additionally estimated vertical vegetation heterogeneity per forest patch. By performing bird point counts, I monitored the community composition of birds and estimated the abundance of insectivorous birds per forest patch. Within the same forest patches, I installed bird exclosures on *Englerophytum natalense* (Sapotaceae, most common tree species throughout) to assess the trophic function of insectivorous birds (in terms of insect herbivore abundances and insect herbivory) along the gradient of forest fragmentation. Forest fragmentation and vegetation heterogeneity altered the community composition of birds. In more detail, forest-dependent insectivorous bird species were associated with low forest fragmentation whereas open-habitat bird species with omnivorous feeding habits seemed to prefer highly fragmented forests. In support, abundances of insectivorous birds decreased with increasing forest fragmentation. Finally, analysis of the findings of the bird exclosures demonstrated the trophic performance of insectivorous birds with lower insect herbivory outside the bird exclosures. Alarmingly, insect herbivory outside the bird exclosures increased with increasing forest fragmentation indicating a loss of the trophic function of insectivorous birds in highly fragmented forests.

Feedback effects via plant responses to herbivory

Plant-herbivore interactions have rarely been viewed from the plant's perspective. However, "bringing the plant back into plant-herbivore interactions" (Karban & Baldwin 1997, p. 100) is vital to fully understand the complex nature of antagonistic plant-herbivore interactions. Plant responses to herbivory include two mechanisms, *i.e.* compensatory growth which enables recovery after herbivory as well as the induced production of defence compounds that have been suggested to deter herbivores from feeding. However, with respect to previous empirical studies there is no consensus on plant responses to herbivory, which may be owed to plant species characteristics and differences in experimental study conditions. Moreover, both mechanisms are nutrient-demanding and thus, costly to plants leading to the assumption that plants favour either growth or defence, particularly at high levels of herbivore and low nutrient availability, termed the *growth-defence trade-off*. By performing a comprehensive meta-analysis, I found that both herbivory and nutrient availability exert strong effects on the performance of plants in terms of compensatory growth and induced defence. My findings show that the plant type (grasses, herbs and woody species) as well as the intensity of herbivory and the temporal scale produce considerable heterogeneity among plant responses. First, at low-intensity herbivory all plant species fully compensated for the loss in aboveground biomass, whereas high-intensity herbivory reduced aboveground biomass. Hence, the degree to which plants fully compensate for lost biomass is determined by the extent of herbivory. In addition, grasses showed a simultaneous decrease in below-ground biomass (irrespective of the intensity of herbivory), which indicates that effects of aboveground herbivory extend to the whole-plant level. Interestingly, natural herbivory induced the production of plant defences, whereas artificially applied herbivory failed to elicit the same plant response. Hence, induced defence in response to herbivory seems to depend on specific cues such as components of insect herbivore saliva enabling economic resource allocation. In contrast to effects of herbivory, effects of nutrient availability on plant growth and defence changed over the course of time showing more pronounced short-term responses. High nutrient availability resulted in a short-term increase in above- and below-ground biomass of grasses and herbs and caused a short-term decrease in defence compounds of herbs and woody species. Presumably, inherently slow growth rates of woody species and the lack of long-term studies circumvented apparent growth effects. However, particularly the pattern in the effects of nutrient availability on herbs support the *resource availability hypothesis*, which suggests that plants reach their optimum growth at low levels of

defence indicating a *growth-defence trade-off*. In support, high nutrient availability diminished the concentration of defence compounds of herbs subject to herbivory. However, overall findings of my meta-analysis imply that nutrient availability rarely altered the effect of herbivory and that growth-defence trade-offs in plants seem to be less common than previously suggested.

Conclusions

Overall, findings obtained in the three studies support the assumption that both context-dependency and the complexity of plant-herbivore interactions may contribute to the discrepancy in findings of empirical studies on plant-herbivore interactions in fragmented forests. In more detail, underlying mechanisms of the effect of forest fragmentation include complex interactive effects of co-occurring environmental drivers as well as multitrophic cascades which mediate the properties of plant-herbivore interactions in fragmented forests. Hence, without considering the environmental context of plant-animal interactions, attempts to unravel the impact of human-driven landscape modifications such as forest fragmentation are prone to lead to biased conclusions. Similarly, plant responses to herbivory have the potential to mediate the outcome plant-herbivore interactions through compensatory growth and induced defence. More specifically, full compensatory growth may blur differences in the feeding pressure of insect herbivores on plants and thus, studies on plant-herbivore interactions that solely monitor the degree of herbivory may easily overlook differences in insect herbivore abundances. Moreover, herbivory-induced production of defence compounds may create feedback effects and thus, alter the composition of insect herbivore communities with potential consequences for the degree of insect herbivory. Hence, plants have to be considered as active counterparts of insect herbivores and thus, have to be incorporated in considerations on effects of human-driven landscape modifications on plant-herbivore interactions.

Findings of the two field studies further show that forest fragmentation has a major impact on forest ecosystems and that the consequences are multi-faceted. In addition to shifts in the community composition and species loss, my results demonstrate that forest fragmentation further interferes with trophic interactions involving multiple trophic levels. In more detail, increasing forest fragmentation altered the community composition of insect herbivores and thereby, diminished the significance of patterns in local tree diversity for insect herbivores. Further, increasing forest fragmentation triggered a trophic cascade beginning with the loss of insectivorous birds, disrupting the trophic control of insect herbivores and ultimately, resulting in increased levels of insect herbivory, which may have serious implications for plant communities. The latter finding additionally reveals that species with similar ecological functions are not necessarily redundant. In contrast, I argue that it is highly likely that species loss is tightly linked to a loss in the ecological function of species. Moreover, I conclude that we have to consider that disturbance-resistant species may not necessarily compensate for the loss of species and maintain the ecological function.

Altogether, I could show that forest fragmentation poses a serious threat to forest communities and trophic interactions and thereby, puts ecosystem functioning and services of forests at high risk. In terms of conservation management, I argue that it is essential to reduce forest fragmentation to a minimum and maintain a network of continuous forests that are well-connected with smaller forest remnants at the landscape scale. This in turn, will benefit species persistence, species migration and recolonization as well as trophic interactions and thereby, ensure species and ecosystem functioning. Likewise, considering the patterns in the findings derived from the meta-analysis may offer management implications, *e.g.* for grassland and forest ecosystems. For instance, alleviated herbivory allows plants to fully recover from herbivory (or artificial defoliation), but may simultaneously maintain plant diversity of grasslands. Additionally, despite short-term benefits for plant growth, high nutrient availability and thus, fertilization or increased nitrogen deposition may not necessarily mitigate effects of herbivory.

To conclude, holistic research approaches that view species and their trophic interactions from different angles as well as consistent advances in ecological research tools (*e.g.* interactive effects, communitiy-level and landscape scale approaches, multitrophic network approaches, meta-analyses in ecology) may contribute to a more comprehensive understanding of the dynamics that structure communities and trophic networks. Both a more holistic view as well as methodological progress in turn, will help to develop effective management implications in order to sustainably maintain functioning and stability of forest ecosystems as well as the services they provide in a human-modified world.

CHAPTER 6

Future research perspectives

Over the last decades, research on the impact of human-driven landscape modifications on plant-herbivore interactions broadened and complemented our knowledge and created a more holistic view on the complexity and vulnerability of ecosystems. However, in search of answers scientists seek to close several scientific gaps while new findings and insights of studies often raise more questions. In my thesis, I addressed implications of deforestation and aimed to unravel consequences of forest fragmentation for species richness, the structure and composition of forest communities, multitrophic interactions and ecological functioning of forest ecosystems. The findings of my thesis provide a more comprehensive view on plant-herbivore interactions in fragmented forest landscapes and particularly highlight the context-dependency and complex character of this antagonistic interaction. Moreover, conclusions derived from my three studies offer practical management implications for forest as well as grassland ecosystems that experience human-driven landscape modifications. However, at the same time, my research revealed a number of new questions that need to be addressed in future research.

Building on findings of my studies, it is essential to pursue long-term studies in order to develop reliable conclusions on the full range of implications following human-driven landscape modifications such as forest fragmentation. In this context, a lot of questions still remain unanswered, *e.g.* does the rate at which species are being lost accelerate over successive years? To what extent does an increase in insect herbivory hamper the reproductive output of plants over the following seasons? And consequently, what changes do we have to expect exactly for the structure and composition of plant communities as well as forest regeneration?

Moreover, recent studies suggest that different plant-animal interactions that share the same partner are coupled and thus, interdependent; for instance, interactions of pollinators and seed dispersers that involve the same plant species (Fontaine *et al.* 2011, Gao *et al.* 2011). As a result of coupled interaction networks, shifts in either interaction network due to landscape modifications may entail direct consequences for interaction patterns of the other network (Albrecht *et al.* 2014). Despite the antagonistic character, shifts in plant-herbivore interactions may similarly contribute to changes in mutualistic plant-pollinator interactions. Studies revealed that insect herbivory affects floral traits and induces flower volatile emissions which may reduce floral attractiveness and thereby, alter pollinator visitation rates (Lucas-Barbosa *et al.* 2011, Rodríguez-Rodríguez *et al.* 2015). Accordingly, floral damage and plant responses that aim at deterring insect herbivores may simultaneously interrupt mutualistic plant-pollinator interactions. As a consequence, this will decrease the beneficial outcome of the mutualistic network for both partners and eventually, amplify effects of insect herbivores on plant reproductive output and thus, plant species persistence (Rodríguez-Rodríguez *et al.* 2015). Similarly, the significance of coupled networks of spatially separated biota that involve plant-mediated interactions (*e.g.* insect herbivores and soil decomposers) has recently been addressed in a review and ultimate implications have been suggested to include changes in pollination services, biological control as well as soil nutrient cycling (A'Bear *et al.* 2014). Hence, further investigations on coupled antagonistic and mutualistic interaction networks are vital, given the potential implications of interdependent shifts in coupled networks.

With my study on trophic cascades between insectivorous birds, herbivorous insects and plants, I could show that functional redundancy is not a general pattern among species that fulfil similar ecological functions within their ecosystem, particularly considering insectivorous birds. However, the significance of insectivorous bats for the trophic control of insect herbivores has increasingly been acknowledged in tropical agroforestry landscapes (*for a review see* Maas *et al.* 2015). Therefore, it may be ecologically worthwhile to explicitly address and disentangle the relative performance of both insectivorous birds and bats in indigenous forests along a gradient of forest fragmentation to get a more comprehensive view on the persistence of this significant ecosystem service in human-modified landscapes.

In addition to human-driven landscape modifications, other environmental drivers such as invasive plant species have been shown to pose a similar threat to biotic communities and ecosystem functioning (*e.g.* Traveset & Richardson 2006). Building on the findings of the meta-analysis, it is necessary to compare the performance of native and exotic plant species at different levels of herbivory and nutrient availability. The success of exotic plants in invading and dominating ecosystems is owed to species-specific character traits (*e.g.* better resource exploitation) that constitute advantages and enable exotic species to outperform native plants. Recent studies for instance, suggest that exotic

species particularly may have a performance advantage in more favourable conditions, *i.e.* high resource availability (Daehler 2003). If so, increasing fertilization and nitrogen deposition in grassland and forest ecosystems may further amplify plant invasions and future studies should therefore, address this issue and search for general patterns (see Burns *et al.* 2007, Li *et al.* 2012, Qing *et al.* 2012).

To build on the findings derived from the meta-analysis, it is inevitable to further unravel the extent of feedback effects of herbivory-induced plant responses on the performance of insect herbivores. Empirical studies found altered feeding preferences as well as reduced growth and reproduction of insect herbivores in response to induced defences. However, the variability of induced responses (*i.e.* across temporal and spatial scales) seems to produce considerable heterogeneity in feedback effects on insect herbivores (Karban 2011; *for an extensive review see* Karban & Baldwin 1997). While it is important to further pursue and unravel patterns in feedback effects on individual insect herbivores, those findings do not allow general conclusions on the performance of populations or diverse insect communities (Karban & Baldwin 1997). Hence, a necessary step and admittedly a challenge for future research will be to unravel patterns in population and community responses of insect herbivores to feedback effects in terms of herbivory-induced plant defences (*but see* Utsumi 2015).

Finally, the maintenance of large forests and their connectivity with smaller forest remnants on the landscape scale is always advisable but may not always be feasible. A compromise and promising alternative may lie in the approach of forest restoration (Ciccarese *et al.* 2012). However, we have to be aware that restored forests are not an equivalent replacement for natural forests and that attempts of forest restoration currently do not compensate for deforestation and forest degradation (Ciccarese *et al.* 2012). Moreover, forest restoration is a highly complex process of assisted forest reconstruction and requires interdisciplinary efforts including local stakeholders (*i.e.* landowners) in addition to scientists and policy makers (Ciccarese *et al.* 2012). Furthermore, scientists still need to elaborate whether restored forests have the capacity to self-reliantly and sustainably maintain diverse forest communities as well as species functional diversity (*e.g.* Hutto *et al.* 2014), which then ensure long-term stability of forest ecosystems and the services they provide in a human-modified world.

CHAPTER 7

Deutsche Zusammenfassung

Anthropogene Eingriffe in natürliche Landschaften, insbesondere die Abholzung und die damit verbundene Fragmentierung von Wäldern, bedrohen Waldökosysteme weltweit. Ausgehend vom heutigen Wissensstand ist anzunehmen, dass sowohl Artengemeinschaften als auch Ökosystemprozesse und die Stabilität von Waldökosystemen stark durch Waldfragmentierung beeinflusst werden. Aufgrund der Komplexität und der dynamischen Variabilität von Waldökosystemen sind die Konsequenzen der Walfragmentierung jedoch nicht absehbar. Dementsprechend ist es essentiell die Folgen der Waldfragmentierung auf Waldökosysteme eingehend zu untersuchen.

Inspiration dieser Dissertation sind widersprüchliche Ergebnisse bisheriger Studien, die den Einfluss von Waldfragmentierung auf herbivore Insekten und das damit verbundenene Ausmaß der Herbivorie untersucht haben. Ursache dieser widersprüchlichen Ergebnisse können kontextspezifische Umwelteinflüsse oder der komplexe Charakter antagonistischer Pflanze-Herbivor-Interaktionen sein. Um Rückschlüsse über die Kontextabhängigkeit von Pflanze-Herbivor-Interaktionen zu ziehen, untersuchte ich den Einfluss von Baumdiversität und der trophischen Kontrolle herbivorer Insekten durch insektivore Vögel mittels zweier Feldstudien in subtropischen Wäldern Südafrikas entlang eines Fragmentierungsgradienten. Des Weiteren untersuchte ich mit einer Meta-Analyse den komplexen Charakter von Pflanze-Herbivor-Interaktionen aus der Pflanzenperspektive. Von besonderem Interesse war hierbei wie Pflanzen sowohl über kompensatorisches Wachstum als auch induzierte Verteidigung auf Herbivorie reagieren und inwieweit dies reziproke Veränderungen in Pflanze-Herbivor-Interaktionen bewirken kann.

Zentrale Ergebnisse

Zunächst wurde deutlich, dass Waldfragmentierung und Baumdiversität Pflanze-Herbivor-Interaktionen über komplexe, interaktive Effekte strukturieren. Zunehmende Baumdiversität in leicht fragmentierten Wäldern führte zu einer Abnahme in der Artenzahl und einer Zunahme der Abundanz herbivorer Insekten. Mit zunehmender Waldfragmentierung nahm dieser Einfluss der Baumdiversität auf herbivore Insekten jedoch ab. Letzteres ist vermutlich auf eine Veränderung in der Zusammensetzung der Artengemeinschaft herbivorer Insekten mit zunehmender Waldfragmentierung zurückzuführen, welche die Sensitivität von Insekten für lokale Unterschiede in der Baumdiversität senkt. Obwohl ich keinen Einfluss auf das Ausmaß der Herbivorie nachweisen konnte, machen die Muster in den Ergebnissen deutlich, dass Waldfragmentierung auf der Landschaftsskala den Einfluss lokaler Faktoren wie Baumdiversität maßgeblich beeinflussen kann. Dementsprechend ist es unumgänglich interaktive Effekte von Umweltfaktoren in Betracht zu ziehen, um das Ausmaß der Konsequenzen von Waldfragmentierung verlässlich abschätzen zu können – auch wenn diese Umweltfaktoren auf unterschiedlichen räumlichen Skalen agieren.

Die daran anknüpfende Feldstudie verdeutlicht, dass zunehmende Waldfragmentierung zum Verlust ökologisch bedeutender Arten führen und dadurch die trophische Kontrolle von herbivoren Insekten stören kann. Im Einzelnen führte zunehmende Waldfragmentierung sowohl zu einer Veränderung in der Zusammensetzung der lokalen Vogelgemeinschaft als auch zu einem Verlust insektivorer Vögel. Des Weiteren zeigte ein Vogelausschluss-Experiment, dass insektivore Vögel in leicht fragmentierten Wäldern das Ausmaß der Herbivorie reduzieren. Allerdings wurde der Einfluß der trophischen Kontrolle herbivorer Insekten mit zunehmender Waldfragmentierung und dem damit einhergehenden Verlust insektivorere Vögel abgeschwächt. Zusammen genommen verdeutlichen die Ergebnisse der zwei Feldstudien, dass der Einfluss von Waldfragmentierung sehr komplex ist und mehrere Trophiestufen involviert. Die daraus resultierenden Konsequenzen sind ökologisch bedeutende Veränderungen in der Zusammensetzung von Artengemeinschaften, der damit einhergehende Verlust artspezifischer Funktionen und potentiell erhöhte Herbivorie.

Schließlich bestätigen die Ergebnisse der Meta-Analyse, dass Pflanzen über kompensatorisches Wachstum und induzierte Verteidigung auf Herbivorie reagieren und auf diesem Weg Pflanze-Herbivor-Interaktionen verändern. Insgesamt betrachtet hing die Pflanzenantwort auf Herbivorie von der Identität der Pflanzen und der Intensität der Herbivorie ab und wies Unterschiede im Zeitverlauf auf. Zunächst war volles kompensatorisches Wachstum von Gräsern, Kräutern, Sträuchern und Bäumen limitiert und erfolgte nur bei geringfügiger Herbivorie. Darüber hinaus führte Herbivorie zeitgleich zu einer Abnahme unterirdischer Biomasse bei Gräsern und hatte somit einen ganzheitlichen Einfluss auf die Pflanzen. Des Weiteren bestätigten die Ergebnisse die Annahme, dass die Produktion von Abwehrstoffen durch spezifische Signale (z.B. Komponenten des Insektenspeichels) induziert wird, was der Pflanze einen ökonomisch sinnvollen Umgang mit Ressourcen ermöglicht. Schließlich

führte eine erhöhte Nährstoffverfügbarkeit kurzzeitig zu verstärktem Wachstum bei Gräsern und Kräutern und zu einer reduzierten Verteidigung bei Kräutern, Sträuchern und Bäumen. Demnach scheinen insbesondere Kräuter unter erhöhter Nährstoffverfügbarkeit ihr Wachstum auf Kosten der Verteidigung zu optimieren, was auf einen *trade-off* zwischen Wachstum und Verteidigung schließen lässt. Letzteres wird dadurch gestützt, dass erhöhte Nährstoffverfügbarkeit den Effekt von Herbivorie auf die Abwehr der Kräuter verringerte. Insgesamt betrachtet scheinen *trade-offs* zwischen Wachstum und Verteidigung jedoch eher selten aufzutreten.

Fazit

Fazit meiner Dissertation ist zunächst, dass kontextspezifische Umwelteinflüsse wie Baumdiversität und Kaskaden über mehrere trophische Ebenen zur Variabilität in Mustern von Pflanze-Herbivor-Interaktionen beitragen können. Und obwohl Pflanzenantworten auf Herbivorie und Nährstoffverfügbarkeit sehr variabel und komplex sind wird jedoch deutlich, dass sowohl kompensatorisches Wachstum als auch die Produktion von Abwehrstoffen durch Herbivorie angeregt werden, was spezifische Muster in Pflanze-Herbivor-Interaktionen gleichfalls beeinflussen kann. Um Konsequenzen anthropogener Eingriffe einschätzen zu können, ist es dementsprechend wichtig, den Umweltkontext mit einzubeziehen und reziproke Effekte innerhalb trophischer Interaktionen zu berücksichtigen.

Insgesamt ist davon auszugehen, dass zunehmende Waldfragmentierung schlussendlich zu erhöhter Herbivorie führt, was sowohl Konsequenzen für das Wachstum und die Fitness von Pflanzen als auch für den Bestand von Arten und die Komposition und Struktur von pflanzenbasierten Ökosystemen haben kann. Darüber hinaus verdeutlichen die Ergebnisse, dass der Fokus von Naturschutzmaßnahmen auf den Erhalt ausreichend großer Waldflächen und deren Verbindung mit kleineren Waldfragmenten auf der Landschaftsskala abzielen sollten. Auf diese Weise können langfristig und nachhaltig Arten und ihre Funktionen im Ökosystem gesichert und somit Ökosystemprozesse und die Stabilität von Ökosystemen aufrecht erhalten werden. Ausgehend von der Meta-Analyse wird deutlich, dass geringfügige Herbivorie volles kompensatorisches Wachstum ermöglicht, während jedoch gleichzeitig die Pflanzendiversität aufrechterhalten werden kann. Und obwohl Pflanzen offentsichtlich von erhöhter Nährstoffverfügbarkeit profitierten wurde gleichzeitig deutlich, dass eine erhöhte Düngung oder zunehmende Stickstoffdeposition nicht zwangsläufig die Effekte von Herbivorie beeinflussen und gegebenenfalls abmildern.

Abschliessend lässt sich sagen, dass sowohl ganzheitliche Forschungsansätze als auch beständiger Fortschitt ökologischer Forschungsmethoden zu einem besseren Verständnis der Mechanismen führen, die Artengemeinschaften und trophische Netzwerke strukturieren. Beides kann in Zukunft die Entwicklung von Managementmaßnahmen vorantreiben, welche Waldökosysteme und ihre Dienstleistungen in anthropogenen Landschaften nachhaltig sichern.

APPENDIX

Chapter 2

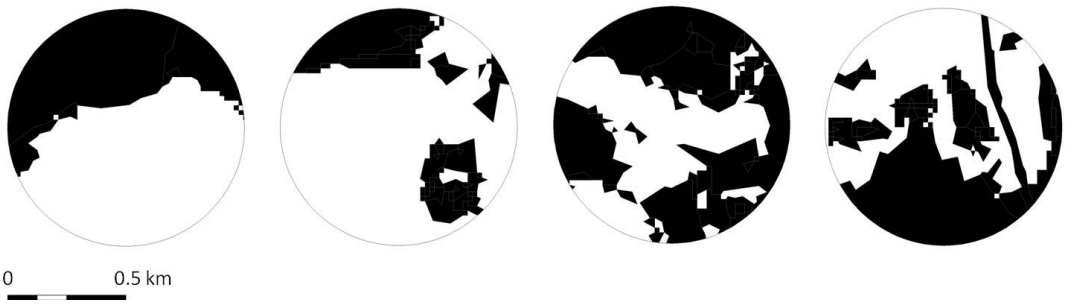
Appendix 2: Focal tree species across the ten study sites.

We selected 67 focal trees across the ten study sites belonging to 29 different tree species from 21 families; selection was based on the proportionate availability of tree species at the individual study sites; we included every tree species of which we found 15 individuals per study site within a range of about 50 m * 50 m; tree species are sorted by frequency of occurrence across the study sites in descending order; the two last rows give the number of selected focal tree species per study site and their overall proportion as part of the tree community per study site.

Tree species	Tree family	Study site										Σ
		1	2	3	4	5	6	7	8	9	10	
Monanthotaxis caffra	Annonaceae		x	x	x	x	x	x	x	x	x	9
Englerophytum natalense	Sapotaceae		x		x	x	x	x	x	x	x	8
Eugenia natalitia	Myrtaceae			x		x		x	x	x		5
Cassipourea malosana	Rhizophoraceae			x					x	x	x	4
Drypetes arguta	Euphorbiaceae			x			x			x	x	4
Peddiea africana	Thymeleaceae		x			x		x		x		4
Allophylus dregeanus	Sapindaceae	x	x		x							3
Chionanthus foveolatus tomentellus	Oleaceae						x	x	x			3
Rapanea melanophloeos	Myrsinaceae	x	x			x						3
Memecylon natalense	Melastomataceae			x					x			2
Ochna arborea	Ochnaceae			x							x	2
Uvaria caffra	Annonaceae							x		x		2
Xymalos monospora	Monimiaceae				x	x						2
Brachylaena uniflora	Asteraceae							x				1
Bridelia micrantha	Euphorbiaceae	x										1
Cassipourea gummiflua	Rhizophoraceae				x							1
Cryptocarya transvaalensis	Lauraceae	x										1
Cryptocarya woodii	Lauraceae									x		1
Euclea natalensis natalensis	Ebenaceae									x		1
Gymnosporia harveyana	Celastracea								x			1
Halleria lucida	Scrophulariaceae	x										1
Nectaropetalum capense	Erythroxylaceae		x									1
Rothmannia globosa	Rubiaceae						x					1
Strychnos henningsii	Strychnaceae			x								1
Strychnos usambarensis	Strychnaceae										x	1
Syzygium guineense guineense	Myrtaceae	x										1
Teclea natalensis	Rutaceae								x			1
Tricalysia capensis capensis	Rubiaceae				x							1
Tricalysia lanceolata	Rubiaceae					x						1
Number of focal tree species per study site		**6**	**6**	**7**	**6**	**7**	**5**	**7**	**8**	**9**	**6**	**67**
Proportion of focal tree species within tree community [%]		**78**	**61**	**74**	**70**	**55**	**47**	**59**	**63**	**52**	**71**	

APPENDIX

Chapter 3



Appendix 3.1: Gradient of forest fragmentation.

We calculated forest fragmentation as perimeter to area ratio of forest fragments (white) within a non-forest landscape matrix (black) for circular study plots (r = 500 m). Exemplary, four study sites with (from left to right) a value of forest fragmentation of 100, 450, 1200 and 2400.

Appendix 3.2: List of bird species monitored during the two sessions of bird point counts.

Bird species are sorted by family in alphabetical order; taxonomy is based on the IOC World Bird List 4.4 (Gill & Donsker 2014); for classification of bird species in guilds (F = frugivorous, I = insectivorous, O = omnivorous) see method section; * indicates the foraging strategy ofinsectivorous bird species that forage within vegetation and directly glean insects from trees; abundance data are given separately for the two monitoring session and in total.

Family	Scientific name	Common name	Guild	Abundance		
				S1	S2	Total
Bucerotidae	*Bycanistes bucinator*	Trumpeter Hornbill	O	1	1	2
	Lophoceros alboterminatus	Crowned Hornbill	O	2	0	2
Campephagidae	*Campephaga flava*	Black Cuckooshrike	I*	1	1	2
Caprimulgidae	*Caprimulgus pectoralis*	Fiery-necked Nightjar	I	1	0	1
Centropodidae	*Centropus burchellii*	Burchell's Coucal	O	5	6	11
Cisticolidae	*Apalis thoracica*	Bar-throated Apalis	I*	10	3	13
	Camaroptera brachyura	Green-backed Camaroptera	I*	29	35	64
	Cisticola natalensis	Croaking Cisticola	I*	0	1	1
	Prinia subflava	Tawny-flanked Prinia	I*	0	1	1
Coliidae	*Urocolius indicus*	Red-faced Mousebird	F	1	0	1
Columbidae	*Columba larvata*	Lemon Dove	F	3	0	3
	Streptopelia capicola	Ring-necked Dove	F	1	0	1
	Streptopelia semitorquata	Red-eyed Dove	F	9	12	21
	Treron calvus	African Green Pigeon	F	2	3	5
	Turtur tympanistria	Tambourine Dove	F	5	8	13
Cuculidae	*Chrysococcyx caprius*	Diederik Cuckoo	I*	1	2	3
	Chrysococcyx cupreus	African Emerald Cuckoo	I*	2	3	5
	Chrysococcyx klaas	Klaas's Cuckoo	I*	5	2	7
	Cuculus clamosus	Black Cuckoo	I*	7	11	18
Cuculidae	*Cuculus solitarius*	Red-chested Cuckoo	I*	15	16	31
Dicruridae	*Dicrurus adsimilis*	Fork-tailed Drongo	I	26	19	45
	Dicrurus ludwigii	Square-tailed Drongo	I	2	2	4
Fringillidae	*Crithagra mozambica*	Yellow-fronted Canary	F	2	1	3

Appendix 3.2 continued

Family	Scientific name	Common name	Guild	Abundance		
				S1	S2	Total
	Crithagra scotops	Forest Canary	F	0	1	1
Lybiidae	*Lybius torquatus*	Black-collared Barbet	O	5	7	12
	Pogoniulus bilineatus	Yellow-rumped Tinkerbird	O	2	1	3
	Pogoniulus pusillus	Red-fronted Tinkerbird	O	0	3	3
Malaconotidae	*Batis capensis*	Cape Batis	I*	18	19	37
	Dryoscopus cubla	Black-backed Puffback	I*	8	13	21
	Laniarius ferrugineus	Southern Boubou	I	30	29	59
	Tchagra tchagra	Southern Tchagra	I*	4	6	10
	Chlorophoneus olivaceus	Olive Bushshrike	I*	0	1	1
	Chlorophoneus sulfureopectus	Orange-breasted Bushshrike	I*	9	0	9
	Telophorus viridis	Gorgeous Bushshrike	I*	0	3	3
Monarchidae	*Terpsiphone viridis*	African Paradise Flycatcher	I*	9	4	13
Motacillidae	*Motacilla clara*	Mountain Wagtail	I	2	0	2
Muscicapidae	*Cercotrichas leucophrys*	White-browed Scrub Robin	I	4	2	6
	Cossypha caffra	Cape Robin-Chat	I*	7	6	13
	Cossypha dichroa	Chorister Robin-Chat	I*	4	12	16
	Cossypha natalensis	Red-capped Robin-Chat	I*	20	10	30
	Muscicapa adusta	African Dusky Flycatcher	I	3	1	4
	Turdus olivaceus	Olive Thrush	O	25	20	45
	Geokichla gurneyi	Orange Ground Thrush	O	1	0	1
Musophagidae	*Tauraco corythaix*	Knysna Turaco	O	18	14	32
Nectariniidae	*Cinnyris chalybeus*	Southern Double-collared Sunbird	O	15	15	30
Nectariniidae	*Cyanomitra olivacea*	Olive Sunbird	O	29	31	60
	Hedydipna collaris	Collared Sunbird	O	0	1	1
Oriolidae	*Oriolus larvatus*	Black-headed Oriole	O	24	21	45
Passeridae	*Passer diffusus*	Southern Grey-headed Sparrow	O	0	3	3
Phasianidae	*Pternistis natalensis*	Natal Spurfowl	O	4	2	6
Phoeniculidae	*Phoeniculus purpureus*	Green Wood Hoopoe	I*	4	3	7
Picidae	*Dendropicos fuscescens*	Cardinal Woodpecker	I*	0	1	1
	Dendropicos griseocephalus	Olive Woodpecker	I*	0	3	3
Ploceidae	*Ploceus bicolor*	Dark-backed Weaver	O	5	0	5
	Ploceus capensis	Cape Weaver	O	2	0	2
	Ploceus ocularis	Spectacled Weaver	O	1	1	2
Pycnonotidae	*Andropadus importunus*	Sombre Greenbul	O	17	25	42
	Phyllastrephus terrestris	Terrestrial Brownbul	I*	6	11	17
Pycnonotidae	*Pycnonotus tricolor*	Dark-capped Bulbul	O	35	31	66

Appendix 3.2 continued

Family	Scientific name	Common name	Guild	Abundance		
				S1	S2	Total
Rallidae	*Sarothrura elegans*	Buff-spotted Flufftail	I*	0	1	1
Rhinopomastidae	*Rhinopomastus cyanomelas*	Common Scimitarbill	I	1	0	1
Sturnidae	*Cinnyricinclus leucogaster*	Violet-backed Starling	O	3	5	8
	Notopholiacorrusca	Black-bellied Starling	O	12	10	22
	Lamprotornis nitens	Cape Starling	O	0	1	1
	Onychognathus morio	Red-winged Starling	O	6	9	15
Sylviidae	*Phylloscopus ruficapilla*	Yellow-throated Woodland Warbler	I*	1	0	1
Trogonidae	*Apaloderma narina*	Narina Trogon	I*	15	9	24
Zosteropidae	*Zosterops virens*	Cape White-eye	O	35	35	70
Abundance				**514**	**497**	**1011**

Appendix 3.3: List of morphospecies of herbivorous insects.

Species identification was based on Scholtz & Holm (2008); as taxonomic resolution for insects in Southern Africa is rather coarse we identified insects as far as possible and further discriminated them into morphospecies (MS, number of MS ≠ number of identified species).

MS	Order	Superfamily	Family	Subfamily	Genus	Species
1	Coleoptera	Chrysomeloidea	Cerambycidae	Cerambycinae		
2	Coleoptera	Chrysomeloidea	Cerambycidae	Cerambycinae	Xystrocera	
3	Coleoptera	Chrysomeloidea	Chrysomelidae	Alticinae	Hermaeophaga	
4	Coleoptera	Chrysomeloidea	Chrysomelidae	Chrysomelinae	Chrysolina	
5	Coleoptera	Chrysomeloidea	Chrysomelidae	Chrysomelinae	Chrysolina	
6	Coleoptera	Chrysomeloidea	Chrysomelidae	Chrysomelinae	Cryptocephalus	
7	Coleoptera	Chrysomeloidea	Chrysomelidae	Chrysomelinae	Gonioctena	
8	Coleoptera	Chrysomeloidea	Chrysomelidae	Chrysomelinae	Jacobyana	*J. sudafricana*
9	Coleoptera	Chrysomeloidea	Chrysomelidae	Cryptocephalinae	Cryptocephalus	
10	Coleoptera	Chrysomeloidea	Chrysomelidae	Eumolpinae	Eumolpus	
11	Coleoptera	Curculionoidea	Anthribidae			
12	Coleoptera	Curculionoidea	Apionidae	Apioninae		
13	Coleoptera	Curculionoidea	Apionidae	Apioninae		
14	Coleoptera	Curculionoidea	Apionidae	Nanophyinae		
15	Coleoptera	Curculionoidea	Apionidae	Nanophyinae		
16	Coleoptera	Curculionoidea	Attelabidae		Parapoderus	*P. nigripennis*
17	Coleoptera	Curculionoidea	Curculionidae	Scolytinae	Hylesinopsis	
18	Coleoptera	Elateroidea	Elateridae	Dendrometrinae	Athous	
19	Coleoptera	Elateroidea	Elateridae	Elateridae	Agriotes	
20	Coleoptera	Elateroidea	Elateridae	Elateridae	Melanotus	

Appendix 3.3 continued

MS	Order	Superfamily	Family	Subfamily	Genus	Species
21	Coleoptera	Scarabaeoidea	Scarabaeidae	Rutelinae		
22	Coleoptera	Staphylinoidea	Scydmaenidae	Clidicinae	Mastigus	*M. transvaalensis*
23	Orthoptera	Acridoidea	Acrididae	Hemiacridinae		
24	Orthoptera	Acridoidea	Pamphagidae			
25	Orthoptera	Tettigonoidea	Tettigoniidae	Tettigoniinae		
26	Orthoptera	Tettigonoidea	Tettigoniidae	Tettigoniinae		

APPENDIX

Chapter 4

Appendix 4.1: List of publications included in the meta-analysis.

Arredondo, J.T. & Johnson, D.A. (2009). Root responses to short-lived pulses of soil nutrients and shoot defoliation in seedlings of three rangeland grasses. *Rangel. Ecol. Manag.*, 62, 470–479.

Barry, K.M., Quentin, A., Eyles, A. & Pinkard, E.A. (2012). Consequences of resource limitation for recovery from repeated defoliation in *Eucalyptus globulus* Labilladière. *Tree Physiol.*, 32, 24–35.

Beaulieu, J., Gauthier, G. & Rochefort, L. (1996). The growth response of graminoid plants to goose grazing in a High Arctic environment. *J. Ecol.*, 84, 905–914.

Burns, J.H., Halpern, S.L. & Winn, A.A. (2007). A test for a cost of opportunism in invasive species in the Commelinaceae. *Biol. Invasions*, 9, 213–225.

Dyer, M., Turner, C. & Seastedt, T. (1991). Mowing and fertilization effects on productivity and spectral reflectance in *Bromus Inermis* plots. *Ecol. Appl.*, 1, 443–452.

Erbilgin, N., Galvez, D.A., Zhang, B. & Najar, A. (2014). Resource availability and repeated defoliation mediate compensatory growth in Trembling aspen (*Populus tremuloides*) seedlings. *PeerJ*, 2, e491.

Eyles, A., Pinkard, E.A. & Mohammed, C. (2009). Shifts in biomass and resource allocation patterns following defoliation in *Eucalyptus globulus* growing with varying water and nutrient supplies. *Tree Physiol.*, 29, 753–764.

Forrester, D.I., Collopy, J.J., Beadle, C.L. & Baker, T.G. (2012). Interactive effects of simultaneously applied thinning, pruning and fertiliser application treatments on growth, biomass production and crown architecture in a young *Eucalyptus nitens* plantation. *For. Ecol. Manage.*, 267, 104–116.

Frost, C.J. & Hunter, M.D. (2008). Insect herbivores and their frass affect *Quercus rubra* leaf quality and initial stages of subsequent litter decomposition. *Oikos*, 117, 13–22.

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Hamilton, E.W., Giovannini, M.S., Moses, S.A., Coleman, J.S. & McNaughton, S.J. (1998). Biomass and mineral element responses of a Serengeti short-grass species to nitrogen supply and defoliation: Compensation requires a critical [N]. *Oecologia*, 116, 407–418.

Han, X., Sistla, S.A., Zhang, Y.-H., Lü, X.-T. & Han, X.-G. (2014). Hierarchical responses of plant stoichiometry to nitrogen deposition and mowing in a temperate steppe. *Plant Soil*, 382, 175–187.

Hartley, S.E. & Amos, L. (1999). Competitive interactions between *Nardus stricta* L. and *Calluna vulgaris* (L.) Hull: The effect of fertilizer and defoliation on above- and below-ground performance. *J. Ecol.*, 87, 330–340.

Hebeisen, T., Lüscher, A., Zanetti, S., Fischer, B.U., Hartwig, U. a, Frehner, M., *et al.* (1997). Growth response of *Trifolium repens* L. and *Lolium perenne* L. as monocultures and bi-species mixture to free air CO_2 enrichment and management. *Glob. Chang. Biol.*, 3, 149–160.

Hódar, J.A., Zamora, R., Castro, J., Gómez, J.M. & García, D. (2008). Biomass allocation and growth responses of Scots pine saplings to simulated herbivory depend on plant age and light availability. *Plant Ecol.*, 197, 229–238.

Houle, G. & Simard, G. (1996). Additive effects of genotype, nutrient availability and type of tissue damage on the compensatory response of *Salix planifolia ssp. planifolia* to simulated herbivory. *Oecologia*, 107, 373–378.

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Hunter, M.D. & Schultz, J.C. (1995). Fertilization mitigates chemical induction and herbivore responses within damaged oak trees. *Ecology*, 76, 1226–1232.

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Appendix 4.2: List of plant species and sample size per response category and species.

AG/BG = above-/belowground; N = nitrogen concentration; stars behind species names depict monocot herbs* (vs. dicot herbs) and shrubs** (vs. trees).

Species	AG biomass	BG biomass	Tannins	Glycosides	Phenolics	N
Grasses						
Achnatherum sibiricum	1					1
Agropyron cristatum	2	1				1
Arrhenatherum elatius	1					
Austrodanthonia bipartita	1	1				
Austrodanthonia setacea	1	1				
Austrostipa oligostachya	1	1				
Avena barbata	1					
Bothriochlora macra	1	1				
Bromus inermis	1					
Calamagrostis epigeios		1				
Carex korshinskii	1					1
Carex ramenskii	1	1				1
Cleistogenes squarrosa	1					1
Deschampsia flexuosa	1					2
Dupontia fisheri	1					
Elymus athericus	1	1				
Eriophorum scheuchzeri	1					
Festuca rubra	2	2				1
Holcus lanatus	1					
Koeleria cristata	1					1
Leymus chinensis	2	1				1
Lolium perenne	3	5				2
Microlaena stipoides	2	2				
Nardus stricta						1
Phleum pratense	2	2				2
Poa bulbosa		1				1
Pseudoroegneria spicata	1	1				
Schizachyrium scoparium	0	1				
Spartina alterniflora	1	1				
Sporobolus kentrophyllus	1	1				1
Stipa grandis	1					1
Stipa occidentalis	1	1				
Themeda triandra	1	1				
Total grasses	**36**	**27**	**0**	**0**	**0**	**18**

Appendix 4.2 continued

Species	AG biomass	BG biomass	Tannins	Glycosides	Phenolics	N
Herbs						
Chromolaena odorata	1	1				
*Commelina bracteosa**	1	1				
Conyza lechleri	1	1				
Erysimum strictum	1	1				
Gnaphalium norvegicum	1					
Heteropappus altaicus	1					
Linnaea borealis	1					1
Lotus corniculatus	1					
*Murdannia simplex**	1	1				
Oenothera odorata	1	1				
Persicaria longiseta		3				
Plantago lanceolata	2	3		6		1
Prunella vulgaris	1					
Solidago chilensis	1	1				
Solidago virgaurea	1					1
*Tradescantia blossfeldiana**	1	1				
*Tradescantia brevifolia**	1	1				
Trientalis europaea	1					
Trifolium repens	2					
Trollius europaeus						1
Urtica sp.	1					
Total herbs	**21**	**15**	**0**	**6**	**0**	**4**
Woody species						
Abies balsamea		2				2
Acacia karroo	1		1			1
Betula pendula	1	3	11	10	1	3
Betula pubescens		1	1		2	1
*Calluna vulgaris***						1
Clausena anisata	1	1				
Diospyros natalensis	1	1				
Dovyalis longispina	1	1				
*Empetrum hermaphroditum***	1					1
Eucalyptus globulus	1	1				1
Eucalyptus nitens	4					
Euclea racemosa	1	1				
Pinus resinosa		1				

Appendix 4.2 continued

Species	AG biomass	BG biomass	Tannins	Glycosides	Phenolics	N
Pinus sylvestris nevadensis	2	2				
Populus tremuloides	3	3	10	5	4	9
Quercus prinus			1		1	
Quercus rubra			2		2	2
*Salix planifolia***		1				
Scolopia zeyheri	1	1				
Teclea gerrardii	1	1				
*Vaccinium myrtillus***	1		1		1	2
*Vaccinium vitis-idaea***	1					1
Total woody species	**21**	**20**	**27**	**15**	**11**	**24**
Overall species total	**78**	**62**	**27**	**21**	**11**	**46**

Appendix 4.3: Formulae for the calculation of effect sizes.

(1.1) Effect size of the main effects of herbivory and nutrient availability

$$d_H = \frac{(M_H + M_{HN}) - (M_C + M_N)}{2s} * J(m)$$

$$d_N = \frac{(M_N + M_{HN}) - (M_C + M_H)}{2s} * J(m)$$

(1.2) Effect size of the interactive effect

$$d_{HN} = \frac{(M_N - M_{HN}) - (M_C - M_H)}{s} * J(m)$$

Here, s is the pooled sampling variance and J(m) is the correction factor for small sample sizes within studies which are calculated as following, with N_i being the sample size and s_i the standard deviation:

$$s = \sqrt{\frac{(N_C - 1)(s_C)^2 + (N_H - 1)(s_H)^2 + (N_N - 1)(s_N)^2 + (N_{HN} - 1)(s_{HN})^2}{N_C + N_H + N_N + N_{HN} - 4}}$$

$$J(m) = 1 - \frac{3}{(4m - 1)} \quad \text{with} \quad m = N_C + N_H + N_N + N_{HN} - 4$$

(2) Sampling variance *s'* for the main and interactive effect of herbivory and nutrient availability

$$s^2(d_H) = \left[\frac{1}{N_C} + \frac{1}{N_H} + \frac{1}{N_N} + \frac{1}{N_{HN}} + \frac{{d_H}^2}{2(N_C + N_H + N_N + N_{HN})}\right]\frac{1}{4}$$

$$s^2(d_N) = \left[\frac{1}{N_C} + \frac{1}{N_H} + \frac{1}{N_N} + \frac{1}{N_{HN}} + \frac{{d_N}^2}{2(N_C + N_H + N_N + N_{HN})}\right]\frac{1}{4}$$

$$s^2(d_{HN}) = \frac{1}{N_C} + \frac{1}{N_H} + \frac{1}{N_N} + \frac{1}{N_{HN}} + \frac{{d_{HN}}^2}{2(N_C + N_H + N_N + N_{HN})}$$

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Erklärung

Hiermit versichere ich, dass ich meine Dissertation mit dem Titel

"Context-dependency and complexity
of plant-herbivore interactions in fragmented forests"

selbstständig und ohne unerlaubte Hilfe verfasst habe. Ich habe mich keiner als der in ihr angegebenen Quellen oder Hilfsmittel bedient und alle vollständig oder sinngemäß übernommenen Zitate als solche gekennzeichnet. Diese Dissertation wurde in der vorliegenden oder einer ihr ähnlichen Form noch bei keiner anderen in- oder ausländischen Hochschule eingereicht und hat noch keinen sonstigen Prüfungszwecken gedient.

Marburg an der Lahn, August 2015

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